Marine Research

SCOTTISH HOME DEPARTMENT

Marine Research
1956 No. 1

The Effect of Electric Fields on Marine Fishes

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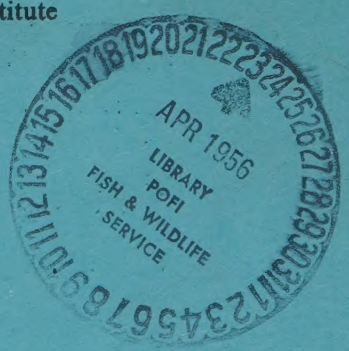

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The reason for this "editorial" note is to welcome a contribution to the Marine Research Series from Dr. Bary of the New Zealand Defence Scientific Corps. Dr. Bary is a New Zealand marine biologist, who was fortunately persuaded to take an interest in the problem of the reactions of fish to electric currents, whilst working for a spell of two years with the National Institute of Oceanography.

The Effect of Electric Fields on Marine Fishes

INTRODUCTION

To obtain electrical control of fish in freshwater lakes and streams a high field strength is required, ause the conductivity of the fish is higher than that of the water, but this is more than offset by the luced current needed to maintain the field strength. Thus the overall power requirement for obning a particular response is comparatively low. Fields of a.c., d.c. and interrupted d.c., or various mbinations of these, have been used for inducing reactions such as electrotaxis and electronarcosis in umber of practical applications (McMillan, 1928, Haskell and Zilliox, 1941, Smolian, 1944, Holmes, 48, Hauck, 1949, Haskell, 1950, Burnett, 1952 and others).

Sea-water, by contrast, has a high conductivity compared with that of the fish so that a high current required to maintain a given field strength and therefore the overall power consumption necessary to luce reactions similar to those obtained in freshwater is greatly increased. Although some experintal data are available on the effects of electric fields on freshwater fish, very few are known for seater.

Because of the paucity of fundamental information, and since rather wasteful empirical approaches the problems involved were already being made, it seemed desirable that controlled, small-scale periments should be carried out as a preliminary to large-scale practical application.

Two general objectives, to obtain basic information, and information which can readily be applied large-scale trials at sea, dominated the experimental approach. To these ends 50 c/s. a.c., d.c. and lsed (interrupted) d.c. were compared for effectiveness in inducing specific reactions in marine fish; d to ensure that the pulse characteristics of pulsed d.c. would be readily reproducible in large-scale ts, the pulses were produced by discharging a capacitor.

Two degrees of electrical control of marine fish are practicable, namely, electrotaxis, or the moving driving) of fish towards the anode in a d.c. field, and electronarcosis, or the 'paralysis' of a fish by electric field. The experiments have been chiefly concerned with these reactions. A third response, erk elicited at make of current (the 'minimum' response), has been used to compare the effects proced when the head of the fish points towards the anode with those when the head is towards the thode in a d.c. field of low strength. The electrical requirements for the reactions have been determined on fish of nearly standard length and on fish of various lengths to obtain an estimate of the effect size; this has involved some 500 experiments and 170 fish.

Because of the very high power output required to gain control of marine fish, neither a.c. nor d.c. practicable in other than tank experiments (Dickson, 1954). Power economies, however, have been und feasible, without loss of effectiveness, by using pulsed d.c. (Scheminsky, 1924; Holzer, 1931; organ, 1951, 1953; Tester, 1952).. Scheminsky stated also that further economy could be achieved reducing the period during which current flows compared with that during which it is off, or in ect, shortening pulse duration. Morgan, and Tester, experimenting in sea-water, demonstrated the idity of this reasoning for pulse durations down to 5.25 ms.

The essentials of these findings by earlier investigators are substantiated by the present study. The crease in power required with diminishing pulse durations continues down to very short pulses for th electrotaxis and electronarcosis, but in both it is progressive and curvilinear with decreasing pulse ration, not linear as described by Scheminsky, Morgan or Tester. There is also an indication when lucing electrotaxis that least power is required at a pulse duration of about 500 μs, and that it increases th either shorter or longer durations.

McMillan (1928) combined results obtained with several species of salmonids and concluded the voltage gradient required to produce electronarcosis was inversely proportional to the lengt fish. After further experimentation on three other species, Holzer (1931) restated this as the 'La Constant Body-Voltage' which claims that the voltage from nose to tail required for a given reac remains constant within a particular species, regardless of the length of individual fish. Kreutzer (1 and Meyer (1952) have deductively extended this theory to include marine fish. Kreutzer (1951), m over, has evolved a formula (see also Meyer, 1952, Kreutzer, 1954) by means of which it is claimed the effective range of the collecting electrode can be calculated for any length and species of fish, vided that the 'body-voltage' is known. In this present study, however, the concept of a constant b voltage has been found not to apply in sea-water; with each of the types of response and electric studied the voltage required increased with the length of fish though the increase was somewhat than directly proportional to the length.

Electrotaxis in d.c. fields has been discussed for freshwater by van Harreveld (1938), and sh to occur in sea-water with *Sardinops caerulea* (Pacific sardine) by Groody, Loukashkin and Grant (19 Groody *et al* used pulsed d.c.: their pulses, which increased slowly from zero and decayed rapidly, w repeated at 5c/s. and had a duration of 133 ms. and an 'off' period of 66 ms. Morgan (1951, 1 and Tester (1952) have also demonstrated electrotaxis with the marine fish *Kuhlia sandvicensis* (aholeh Meyer (1952) has reported the successful application of electrotaxis in field trials: freshly caught Ba herring, 20 cm. long, were dropped into a field of pulsed d.c. between electrodes 40 m. apart and 'dr in' over a radius of 10 m.; 40 cm. cod reacted in the same way over a 15 m. radius. His pulses w triangular with a peak voltage of 2000 V. (10,000 to 15,000 A.), of 2 ms. duration and repeated frequency of 20 c/s. German workers believe (Peglow, personal communication, and see Hous 1949), and Groody *et al.* imply, that fish length needs to be considered in inducing electrotaxis; Peg stated that it is necessary to match the pulsing frequency with the rapidity of the swimming m ments of the fish, and hence shorter fish required higher frequencies.

Results from the present study have demonstrated that with triangular-shaped pulses (capac discharges, similar to those used in the German field trials) frequencies as high as 20 c/s. and puls the length given by Groody *et al.* are not necessary. In fact, electrotaxis was induced at durations f 120 to 9000 μs and at frequencies of 2 to 21 c/s. I have not yet had an opportunity to study how frequencies needed to induce electrotaxis depended on the length of fish.

It has been found during the present work that, to induce either electrotaxis or electronar with pulsed d.c., five variable factors need to be considered; three are independent, namely, p duration, frequency of pulsing and fish length, and alteration of any one of these involves a compensa alteration in the other two to obtain a given response. These, the power and the voltage gradient, dependent on the previous three factors.

Approximately constant relationships exist between the a.c. and d.c. voltage gradients (and pow required for inducing a particular reaction, and between the gradients and powers of either a.c. or for producing the several responses. There is also a constant relationship between the effectivenes d.c.— (with the head pointing towards the cathode) and d.c.+ (with the head pointing towards anode) for inducing the minimum response.

Changing temperature does not appear to affect the voltage gradient of a.c. or d.c. needed f particular response, nor does length of time in captivity, but 'fatigue' requires an increase in grad to elicit the minimum response.

MATERIAL AND METHODS

All experiments were carried out in sea-water of salinity 33 to 34‰. The pulsed d.c. experime on which emphasis has been placed, were performed entirely with golden grey mullet (*Mugil aur* Risso); for a.c. and d.c. these were supplemented with bass (*Marone labrax* (L.)) and flounder (*Platich flesus* (L.)).

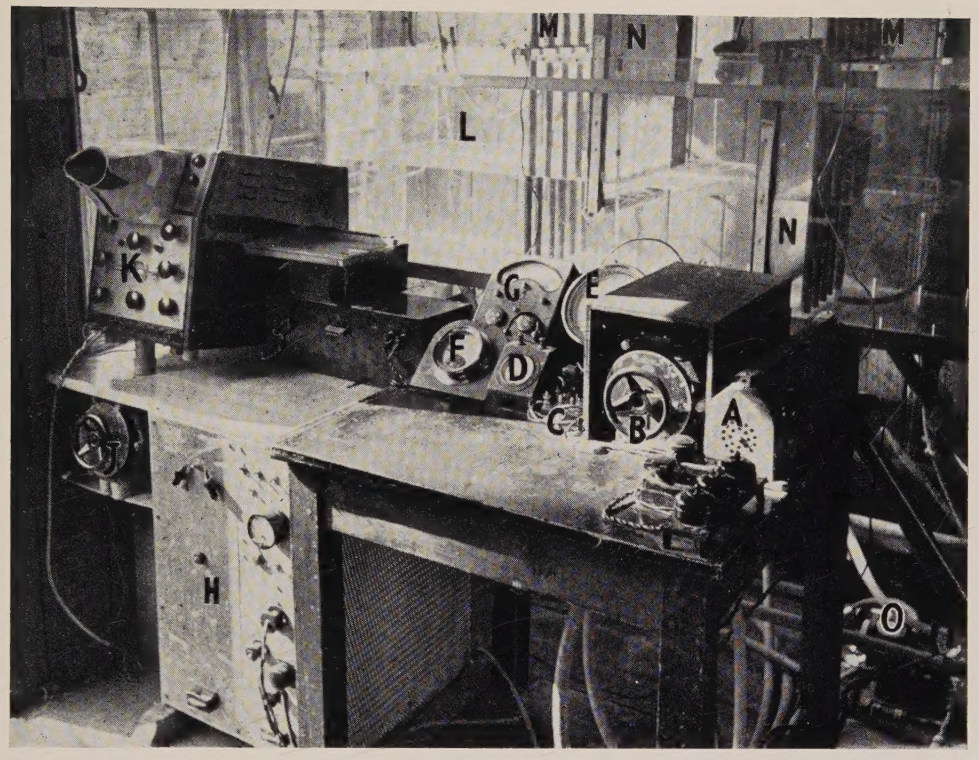


Fig. 1. *Experimental Apparatus*

A. d.c. rheostat
B. a.c. 'Variac' variable-ratio transformer
C. reversing switch
D. E. d.c. voltmeter and ammeter
F. G. a.c. voltmeter and ammeter
H. pulse-generator unit
J. 'Variac' in supply line to pulse generator
K. cathode-ray oscilloscope
L. perspex tank
M. electrode banks
N. towelling screens
O. outflow pump

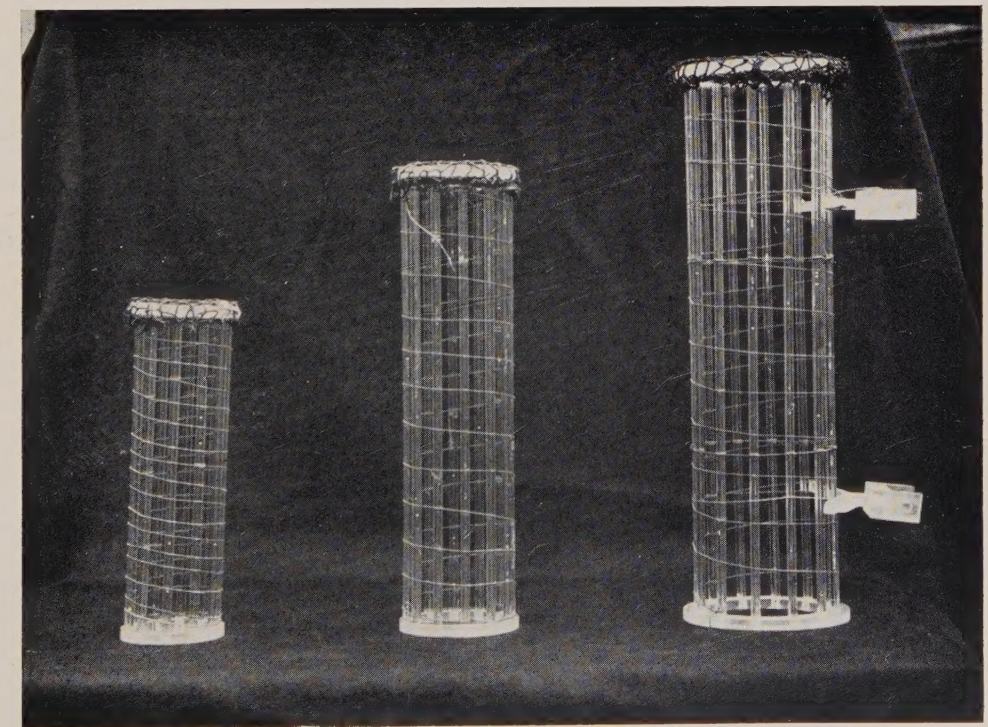


Fig. 2 Glass-rod cages for holding fish in the minimum-response experiments. That on the right has part of the adjustable mount attached. Retaining nets are placed on the upper end of each cage.

The perspex experimental tank (Fig. 1) was 180 cm. long and 43.8 cm. square, internal cross section, l in it the water depth was maintained at 20 cm. For minimum-response and electrotaxis experiments, electrodes were kept 160 cm. apart, and for electronarcosis, 60 cm. apart. During experimentation, h filtered sea-water was pumped into the middle portion of the tank from Haslar Creek, an arm of rtsmouth Harbour. An electric pump, controlled by a mercury switch, regulated the water level by wing water from both ends, which thereby minimized contamination from the electrolysis products lved when using d.c. Each electrode consisted of a bank of six high-quality carbon rods, 1.8 cm. meter, 7.2 cm. apart at their centres and mounted in deep brass rings (which also formed the contact face) set on a perspex strip; when in use the rods almost touched the bottom of the tank. Towelling eens served the double purpose of separating the electrodes from the central section and of delaying diffusion of electrolysis products towards this section. Tests with probe electrodes, insulated except their tips, and a valve-voltmeter showed the field to be uniform between the screens. The effective ctrode area, therefore, was taken as the cross-sectional area of the tank.

It was necessary frequently to clean both electrode rods and brass contact-mounts; rods were dipped dilute hydrochloric acid, in fresh water and wiped down; the mounts were cleaned with very fine ery paper. All exposed soldered joints or contacts subject to corrosion by sea-water were cleaned iodically or renewed. To check that the electrodes, all contacts and the water in the tank were con-cting normally, resistance was determined with a.c. prior to and during experiments.

The d.c. supply, from a bank of 'NiFe' accumulators kept on charge during use, passed through a iable resistance and ammeter to the electrodes at which a maximum of about 30 V. was available. means of a reversing switch electrode polarity could be reversed. Fifty-cycle a.c. (230 to 240 V.) fed through a 'Variac' variable-ratio transformer, a fixed-ratio step-down transformer and an meter, with an available potential of up to 30 V. at the electrodes.

Pulsed d.c. was obtained from a pulse generator designed and built by the National Institute of eanography. The pulses were produced by charging a bank of electrolytic capacitors from a d.c. rce through one thyratron, and discharging them through the tank using a second thyratron. The iable-voltage d.c. supply was obtained from a full-wave metal rectifier with a large smoothing capaci- across its output and supplied with 50 c/s. a.c. through a 'Variac' variable-ratio transformer. The ratrons were fired by pulses from a multivibrator master-pulse generator, enabling the pulse repetition e to be set to pre-determined values between about 1 and 700 c/s. Pulse duration was varied by tching capacitors into or out of the main bank. Pulses were triangular in form, rising sharply from o and decaying exponentially, and were adjustable by small increments from 65 to 9000 μs in duration. se duration, defined as the time between start of the pulse and the point where the voltage falls to of the peak value, i.e., at 0.37 of the height from the base-line, was measured by a cathode-ray lloscope connected across the electrodes; peak voltage was determined from the height of the peak n the base-line, and frequency could be checked by reference to the time-base.

Power for pulsed d.c. was calculated from the formula $\frac{T}{2R} V^2F$

where T = pulse duration in seconds
R = resistance in ohms
V = peak voltage
F = frequency of pulsing in cycles per second.

The voltage gradient in the centre section of the tank may be calculated from the voltage between electrodes, if allowance is made for polarization effects and for the increase in gradient near and on electrodes caused by the crowding of the lines of current flow. The latter is most conveniently ex-sed as an equivalent δ added to the separation of the electrodes and is independent of electrical litions and of the actual separation of the electrodes. With a.c., δ was found by experiment (and calculated) to be less than 0.5 cm., which was considered negligible. The total of the equivalent

δ and of polarization effects under typical experimental conditions was found to be approximately which was accepted as within experimental error and neglected. With pulsed d.c. or d.c., polariza effects were considerably greater; the method of measurement of pulsed d.c. automatically took acc of polarization, and when d.c. was used, it was allowed for by measuring the back e.m.f. immedia on breaking the circuit and subtracting it from the measured voltage.

Fish were caught by seining and were kept for periods up to six weeks before experimenta in order to eliminate damaged specimens and to acclimatize the remainder to conditions and die captivity. Storage tanks for the fish were outdoors, fitted with aerators and thermostatically-contro heaters and their water could be changed as necessary.

Experiments are reported for two separate groups of mullet. The first, the Standard Fish, v taken in a single haul and were kept together in the tanks; they were of one age group and were betv 18.5 and 20.6 cm. long. Group 2 Fish were caught over a period of twelve months and ranged in le from 8.6 to 30.2 cm. Usually fifteen to twenty specimens of Group 2 were available for experimenta at any one time.

To determine the degree of stimulation, three reactions were used as end-points, namely, the m mum response, electrotaxis and electronarcosis.

In the minimum-response tests the jerk can be consistently elicited at make, or more rarely at br of the circuit at low field strengths. Other sporadic responses may precede it, but the jerk which characteristic and reproducible in the seven or eight species of fish tested was taken as the minir observable reaction. It was of value for differentiating between the effectiveness of a.c. and d.c. within the effects of d.c., between that when the head of the fish was towards the anode (d.c.+) when it was towards the cathode (d.c.—). Individual fish were placed in cylindrical cages of glass (Fig. 2), mounted in perspex rings, with the open ends closed by cotton netting. Cage and fish suspended from perspex supports between the electrodes, and because the fish was unable to turn in cage it could be held in an almost constant position relative to the field. Five or six responses averaged from each fish, which reduced effects due to small movements of the fish. Tests with p electrodes and a valve-voltmeter showed no detectable distortion of the field within the cage.

In electrotaxis experiments individual fish were permitted to swim freely. Firm control was sidered to be obtained when, in two or three runs up and down the tank, the fish consistently hea towards the anode and reversed direction when electrode polarity was reversed. Experiments carried out with d.c. and pulsed d.c.

A similar procedure was adopted for determining the electrical requirements of a.c., d.c. and pu d.c., when inducing given reactions. In general outline, one fish was subjected to a series of shoc increasing strength until the desired response was elicited; the first one or two shocks were less thar voltage gradient shown by a preliminary test (on another fish) to be approximately that needed fo purpose.

In electronarcosis experiments, the shocks in a series were each of 5 sec. duration, and 1 min. inte separated successive shocks. To be acceptable the reaction had to be completed between 2 and 4 (by stopwatch) after closing the circuit and at the third, fourth or fifth shock of a series. At a sele pulse duration and frequency, peak voltage was increased after each shock of the series until ele narcosis resulted. Pulse durations were spaced conveniently; with Standard Fish they were 115, 550, 875, 1500, 2000, 3000 and 4000 μs, and with Group 2 Fish, 83, 110, 250, 550, 1500 and 200 At a given duration, fish were subjected to shocks at each of the frequencies 10 (except for shortest p durations), 14, 21, 30, 41 (not beyond 41 c/s. for durations of 3000 and 4000 μs), 60, 84 (not be 84 c/s. for durations of 1500 and 2000 μs), 122, 172 and 248 c/s., or for shortest durations up to 60 The restriction on the rate of pulsing at longer pulse durations was imposed by the design of the cir

For electrotaxis experiments the frequencies 2.07, 2.88, 4.2, 6.05, 7.2, 10 and 21 c/s. and the pulse urations of 120, 240, 500, 1000, 5000 and 9000 μs were used. The procedure adopted in experiments as similar in essentials to that for electronarcosis. Shocks of increasing strength were administered series, but the 5 sec. shock period could be adhered to only until electrotactic control was almost tablished. Thereafter this period was necessarily lengthened in order to determine that control was rm. Intervals between these later shocks were increased from 1 to 3 or 4 min. to ensure a reasonable egree of recovery from possible 'fatigue' effects.

The minimum response occurs with make of current so that prolonged exposure is unnecessary; or does the interval between shocks need to extend beyond 30 sec. Otherwise the procedure followed iat already outlined.

Results have been considered only for fish which appeared to be healthy at the time of experimenting.

EXPERIMENTAL RESULTS

LTERNATING AND DIRECT CURRENT

The electrical requirements for eliciting the minimum response, electrotaxis and electronarcosis eactions using a.c., d.c. and (in some instances) pulsed d.c. are discussed below as potential difference long the fish. It has been assumed (although not quite accurately) that the voltage per centimetre ultiplied by the fish length is the equivalent of the voltage over the fish. Since the conductivity of the ea-water is higher than that of the fish, the actual voltage drop must of course be somewhat higher Holzer, 1931); but as it is difficult to measure the actual potential difference over a free-swimming fish, nd since, in field trials, potential between the electrodes is readily obtainable, the assumption has been iade.

In Fig. 3 potential difference along the fish is plotted against fish length for the minimum response nd for electrotaxis (lower four curves), and in Fig. 4 for electronarcosis (lower two curves). Positions f the lines are calculated by the least-squares method and are the regression of y, the potential difference long the fish, upon x, the length of the fish.

TABLE I

Comparative Effectiveness of A.C. and D.C. for Inducing the Minimum Response and Electronarcosis in a 20-cm. Fish

Reaction	Current	Potential Over Fish (Volts)	Power (W/cu.m.)	Ratios of Effectiveness: Voltage	Ratios of Effectiveness: Power
Minimum Response	a.c.	0.50	22	1.0	1
	d.c.—	0.89	69	1.8	3
	d.c.+	1.78	277	3.6	13
Electro-narcosis	a.c.	2.75	662	1.0	1
	d.c.	5.71	2853	2.1	4

Table I shows the comparative effectiveness of a.c. and d.c. for inducing the minimum response and ctronarcosis in a 20 cm. fish. To induce the minimum response, a.c. requires rather more than half e potential difference of d.c.— and rather more than one-quarter that of d.c.+, i.e., a.c. is almost ice as effective as d.c.— and almost four times as effective as d.c.+ When inducing electronarcosis th free-swimming fish, the distinction between d.c.+ and d.c.— is lost but the values obtained suggest at d.c.— effect is dominant; this is shown by the fact that the ratio of 1.0 to 2.1 (Table I) is nearer the tio between a.c. and d.c.— (1.0 to 1.8) than that between a.c. and d.c.+ (1.0 to 3.6) in minimum-ponse tests. The increase of the d.c. ratio for electronarcosis over that of d.c.— for the minimum

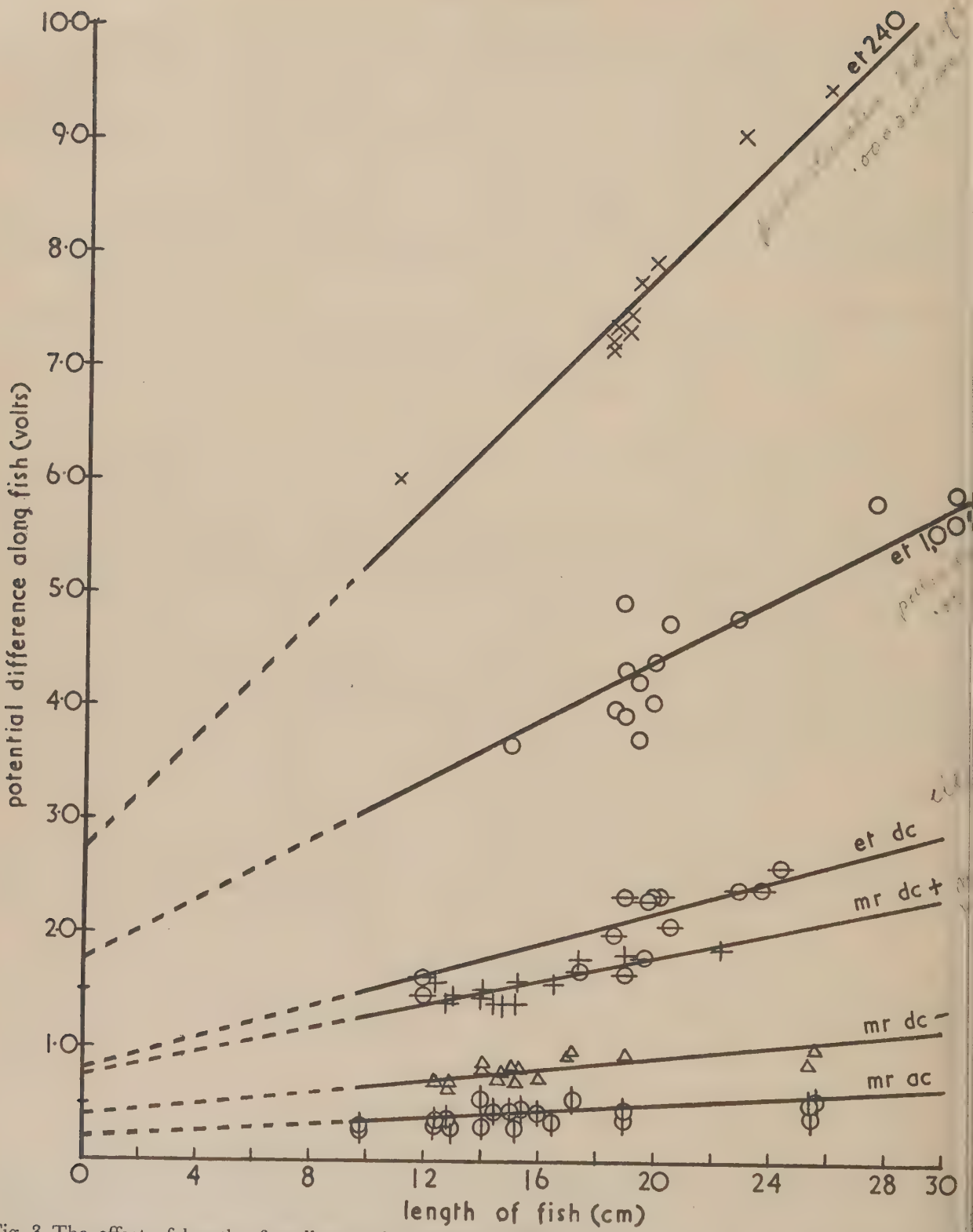


Fig. 3 The effect of length of mullet on the potential difference between nose and tail required to indu
electrotaxis (*et*) and the minimum response (*mr*).
et 240, et 1,000: electrotaxis at pulse durations of 240 and 1000 μs respectively.
et d.c.: electrotaxis with d.c.
mr d.c.+, *mr d.c.−*: minimum response with d.c.+ and d.c.− respectively.
mr a.c: minimum response with a.c.

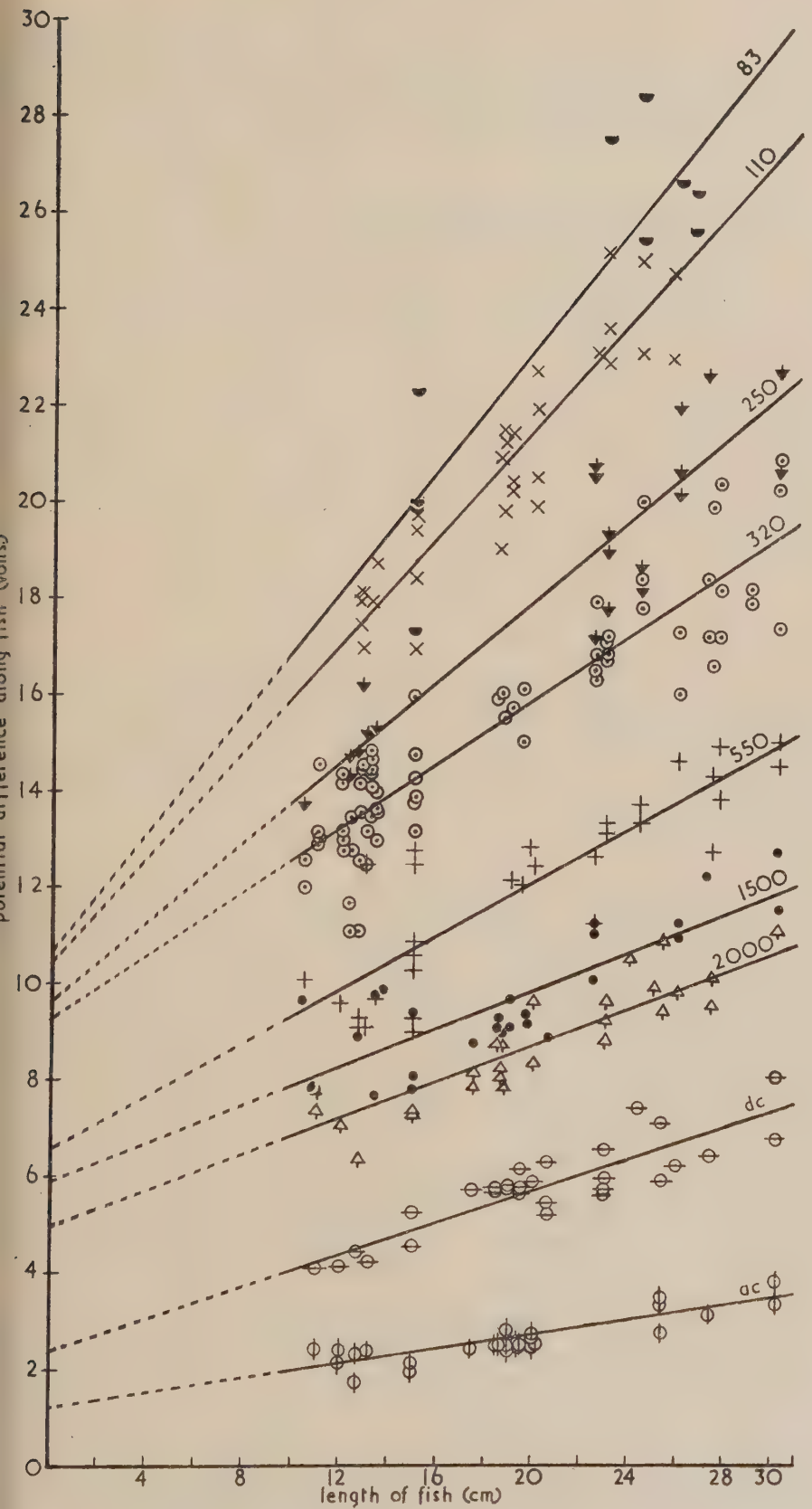


Fig. 4 The effect of length of mullet on the potential difference between nose and tail required to induce electronarcosis when using pulsed d.c. at pulse durations between 83 and 2000 μs and also using d.c. and a.c. The pulse duration in microseconds is shown on the appropriate line.

response suggests that in electronarcosis there is a persisting tendency for the fish to head towards anode. There is a striking difference in the power requirements between d.c. and a.c.; for induc electronarcosis a fourfold increase occurs when using d.c. instead of a.c., while to induce the minim response, d.c.— requires three, and d.c.+, thirteen, times the power needed with a.c.

TABLE II

Comparative Voltage and Power Requirements for Minimum Response, Electrotaxis and Electronarcosis for either A.C. or D.C. in a 20-cm. Fish

Reaction	Current	Potential Over Fish (Volts)	Power (W/cu.m.)	Ratios of Requirements	
				Voltage	Power
Minimum Response	a.c.	0.50	22	1.0	1
Electrotaxis	—	—	—	— :	— :
Electro-narcosis	a.c.	2.75	662	5.6	30
Minimum Response	d.c.—	0.89	69	1.0 :	1 :
Electrotaxis	d.c.	2.10	386	2.4 :	6 :
Electro-narcosis	d.c.	5.71	2853	6.4	41

A second series of relationships is demonstrated in Table II, where potential difference along fish needed to elicit the minimum response is compared with that for electronarcosis for either a.c. or Although the potentials for the two responses differ widely, the ratios of the requirements range betw only 1 : 5.6 and 1 : 6.4. Again the higher d.c. values are probably the result of persistent anodic eff For the electrotaxis reaction, potential and power quantities of d.c. are intermediate between those the minimum response and electronarcosis.*

A.c. is more efficient (on r.m.s. values) than d.c. for inducing electronarcosis in marine fish, bu is at the same time more severe. Under the influence of an increasing a.c. field fish become very distres and agitated and strongly attempt to avoid the field. If the increase is gradual, 'oscillotaxis', or taking up of a position with the body axis at right angles to the field direction, occurs (see also Harreveld, 1938), but on further increase respiratory movements cease, the opercula flare widely, and fish becomes rigid and then sinks. If the circuit is broken immediately paralysis is obtained, recov is fairly rapid; mobility can be delayed for 30 mins. or more by prolonging paralysis for a few minut When swimming recommences the fish is usually abnormally sluggish and reacts only slowly, or not all, to such stimuli as gentle prodding, bumping the tank or waving something white nearby. N cosis with d.c., on the other hand, is milder in all respects. The fish becomes immobile and sinks, bu flaccid; there is an initial cessation of respiratory movements and the opercula flare. If exposure to current is prolonged, respiratory and other movements will recommence on breaking the circuit a may do so beforehand. In contrast to the a.c. after-effects, the fish following d.c. narcosis appears react more strongly than normal to external visual and tactile stimuli.

Severe, repeated shocking with a.c., d.c. and pulsed d.c. failed to cause detectable internal hæm rages or injuries to muscles, bones, etc., as have been described as occurring in experiments with fr water fish using a.c. (Hauck, 1949). On occasion a temporary bleeding from the region of the g occurred if paralysis was suddenly induced with a.c. or pulsed d.c., but no other effects were observ

*Although distances of 60 cm. separated the electrodes for the experiments on electronarcosis and 160 cm. for those on electrot and minimum responses, the power per cubic volume needed to induce a given reaction over both distances was practically identi When, with other conditions remaining equal, the electrodes are moved apart, the resistance between them increases proportion with distance, from 1.91 to 5.1 ohms; the wattage needed also increases proportionally but power per cubic metre does not. I therefore, directly comparable over the two distances.

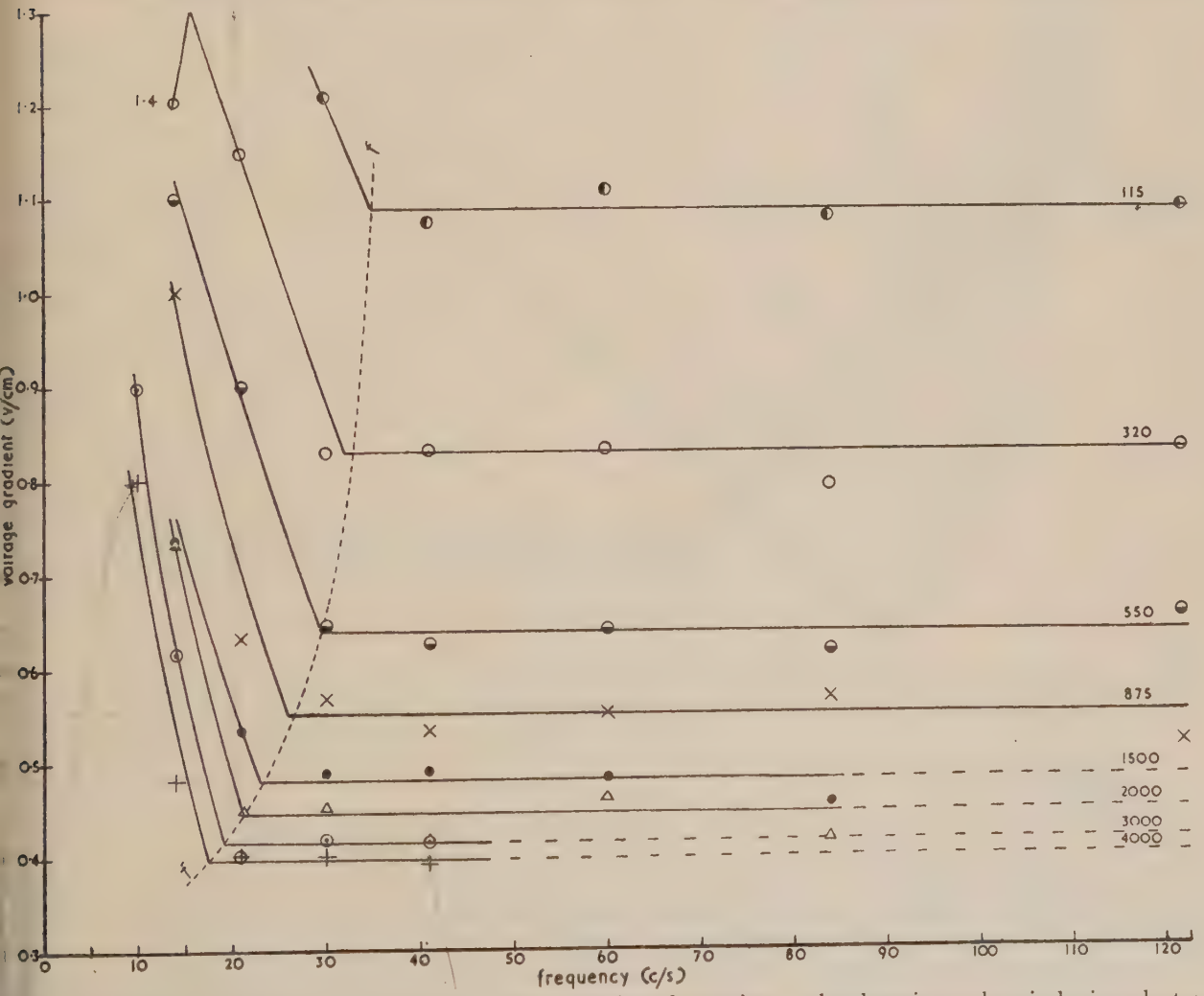
ULSED D.C.

To induce a given reaction using pulsed d.c., three independent variables, namely, fish length, ulse duration and frequency of pulsing, must be considered. Two other factors, voltage gradient and ower, are dependent on the values of these. Fish length directly affects the voltage gradient required o elicit a given response at a given frequency and pulse duration, and has been the subject of separate xperimentation; it is considered later.

The relationships of the other four variables have been determined under conditions as near constant s were obtainable. Standard Fish only were used; temperature was kept to between 9° and 10°C; ater depth and distance between the electrodes was maintained at 20 cm. and 60 cm. respectively, nd experiments carried out only when the resistance of the circuit was within 3% of the value appropri-te to the temperature (1.91 to 1.95 ohms for the range 9° to 10°C).

The inter-relationships of the variables are shown in detail in Figs. 5-7 for electronarcosis and 8-10 or electrotaxis; the power variations for inducing both reactions are shown in Fig. 11. It must be mphasised that, when inducing a particular reaction, alteration of any one factor involves alteration f the others.

(*a*) *Electronarcosis.* The effect of frequency of pulsing on the voltage gradient required for electro-



g. 5 The effect of frequency of pulsing on voltage gradient for various pulse durations when inducing electro-narcosis in Standard Fish (mullet) with pulsed d.c.
The pulse duration in microseconds is shown on each curve.
ff: the optimum-frequency curve.

narcosis for the several pulse durations used is demonstrated in Fig. 5, and these data are converted watts per cubic metre and again plotted against frequencies in Fig. 6.

In the curve of each pulse duration (Fig. 5) there is a frequency at which a sudden change* in t direction of slope occurs. Towards frequencies lower than this 'optimum frequency', the necessa voltage gradient increases markedly, but at higher frequencies there is no detectable change in t gradients required, nor was there for frequencies up to 500 or 600 c/s. (not plotted).

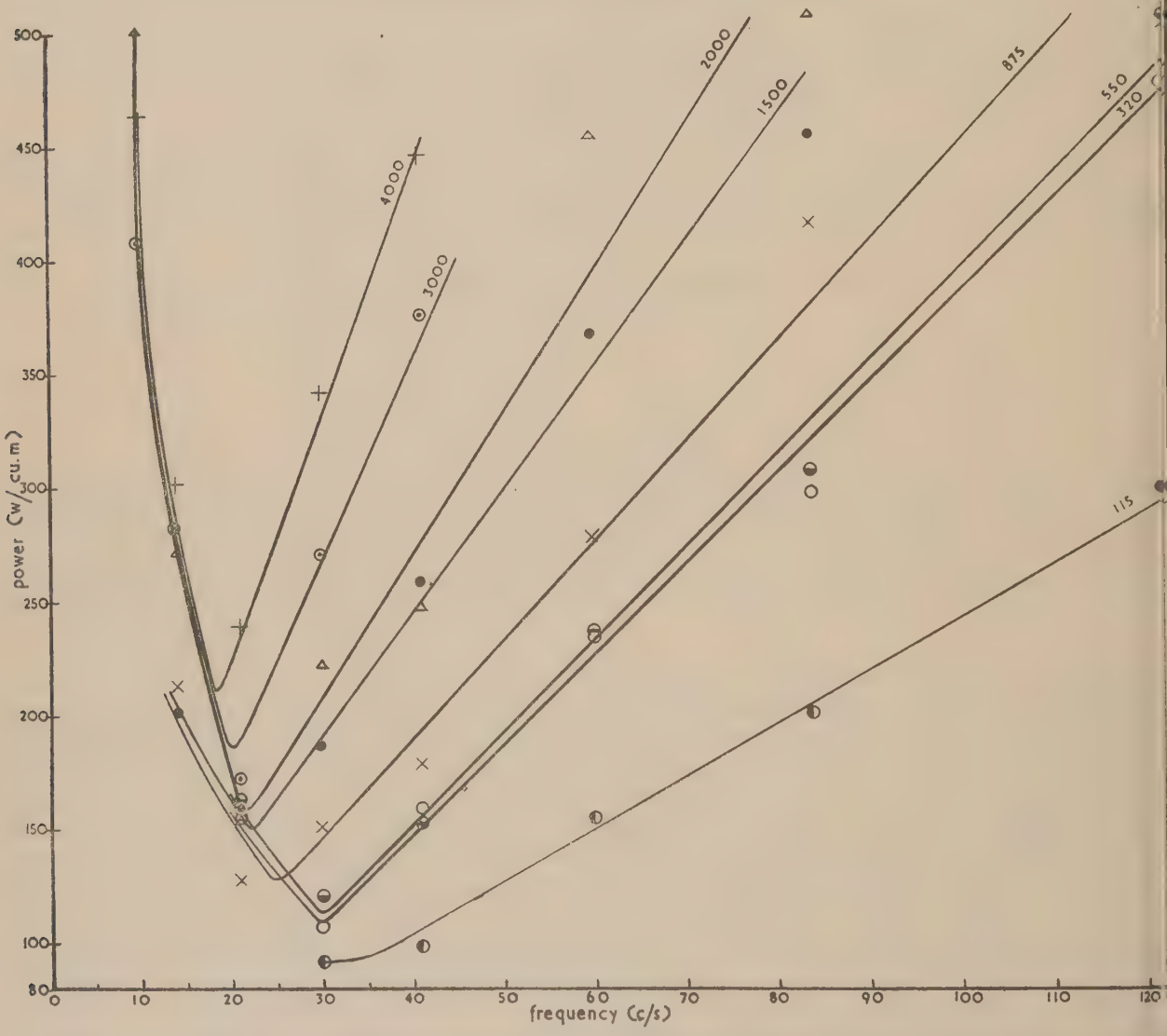
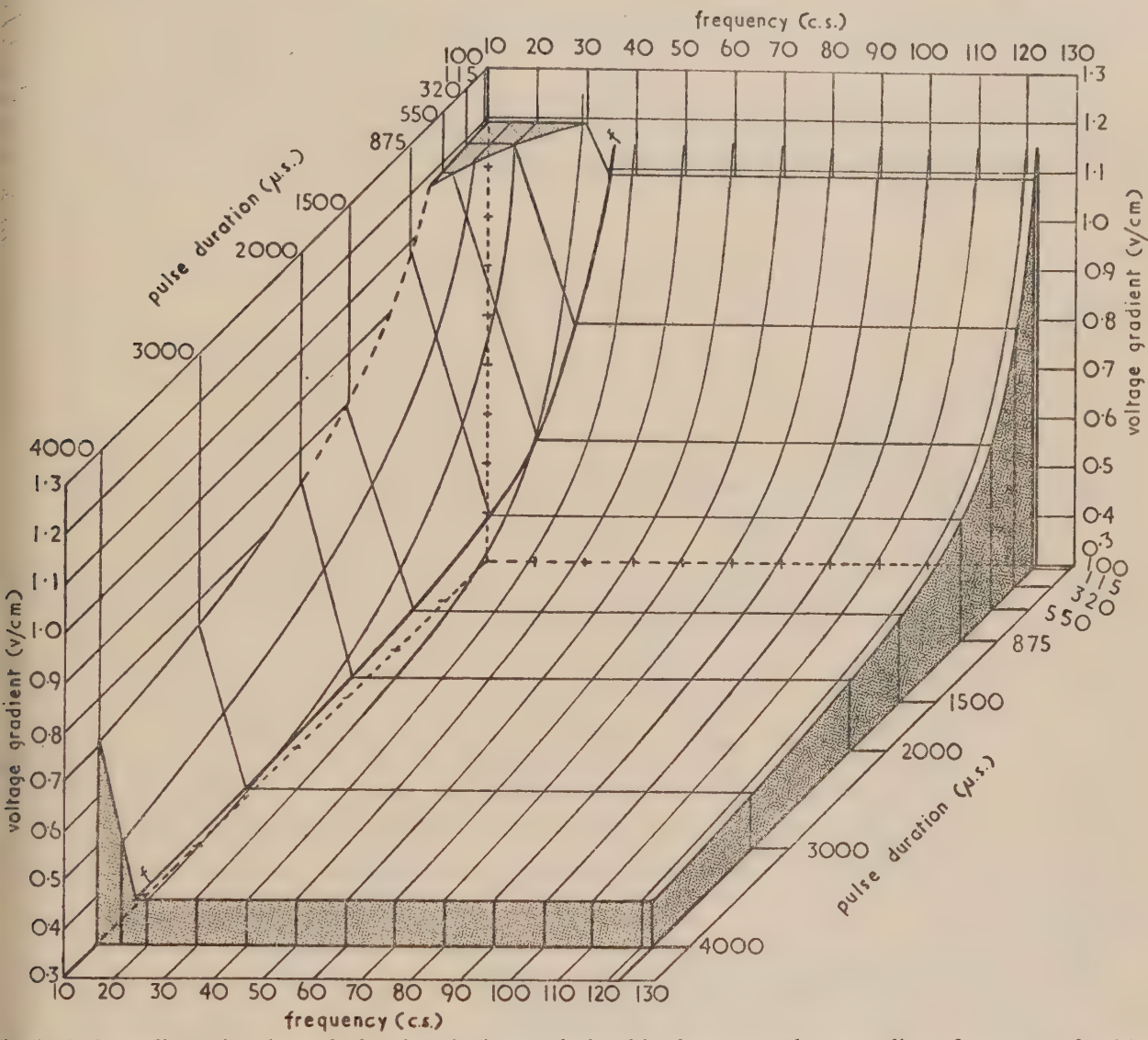


Fig. 6 The effect of frequency of pulsing on the power needed to obtain electronarcosis in Standard mullet w pulsed d.c.
The pulse durations used are the same as in Fig. 5 and are shown on the curves.

The optimum frequency is significant as that of lowest power output for inducing electronarco at a particular pulse duration (see Fig. 6), and it decreases as pulse durations are lengthened. At 115 it is 35 c/s., and the almost vertical trend of the optimum frequency curve (Fig. 5, *ff*) suggests that would increase only very slightly at shorter durations; at 4000 μs the optimum frequency has decreas to 17.5 c/s. and it is evident that as pulses become longer it will become progressively less. The su

*The onset of this change of slope (the optimum frequency) may not be in fact as angular as illustrated in Figs. 5 and 8, bu aid in interpretation and because of the few points in each curve, the practice of demonstrating the change as a sudden one was retain

cessive minima in Fig. 6 demonstrate the same relationships. Both Figs. 5 and 6 show opposed trends for pulse duration and the voltage gradient required for electronarcosis: as the pulse is shortened the voltage gradient required increases, the increase being proportionately less than the amount of shortening in the pulse duration.



ig. 7 A three-dimensional graph showing the inter-relationships between voltage gradient, frequency of pulsing and pulse duration when inducing electronarcosis in Standard mullet.
The figure is constructed from curve values of figure 5.
ff: the optimum-frequency curve.

The relationships of pulse duration, frequency and voltage requirements are demonstrated in ig. 7, a three-dimensional graphic representation in which they are plotted against each other for a tandard Fish. Within the limits of the data, any combination of these variables for inducing electro-arcosis may be read off. The optimum frequency curve, *ff*, is seen to shift towards the right, cutting ıccessively the frequency curves of 20 and 30 c/s. as shorter durations are reached. At the same time, ıe increase of voltage gradients with shortening of pulse is apparent in the steepening of all the frequency urves towards the 'back' of the figure.

The calculated power output for optimal electronarcosis is the result of combined effects of the ulse duration, frequency and voltage gradient needed to induce the reaction. It increases as pulse

duration is lengthened (Fig. 11, *en*), even though lowered frequencies and voltage gradients are requir The increase appears to be curvilinear with a tendency towards lessening in rate of increase at lon durations.

Evidence in support of this tendency is afforded by the flattening of the electrotaxis curve (*et*) longer durations than were used for electronarcosis.

(*b*) *Electrotaxis.* Except that the reaction is induced at a generally lower level of electrical requi ment, the results from electrotaxis experiments with the Standard Fish are closely comparable to th for electronarcosis. In Figs. 8-11 experimental data for electrotaxis are treated in a manner simila those for electronarcosis.

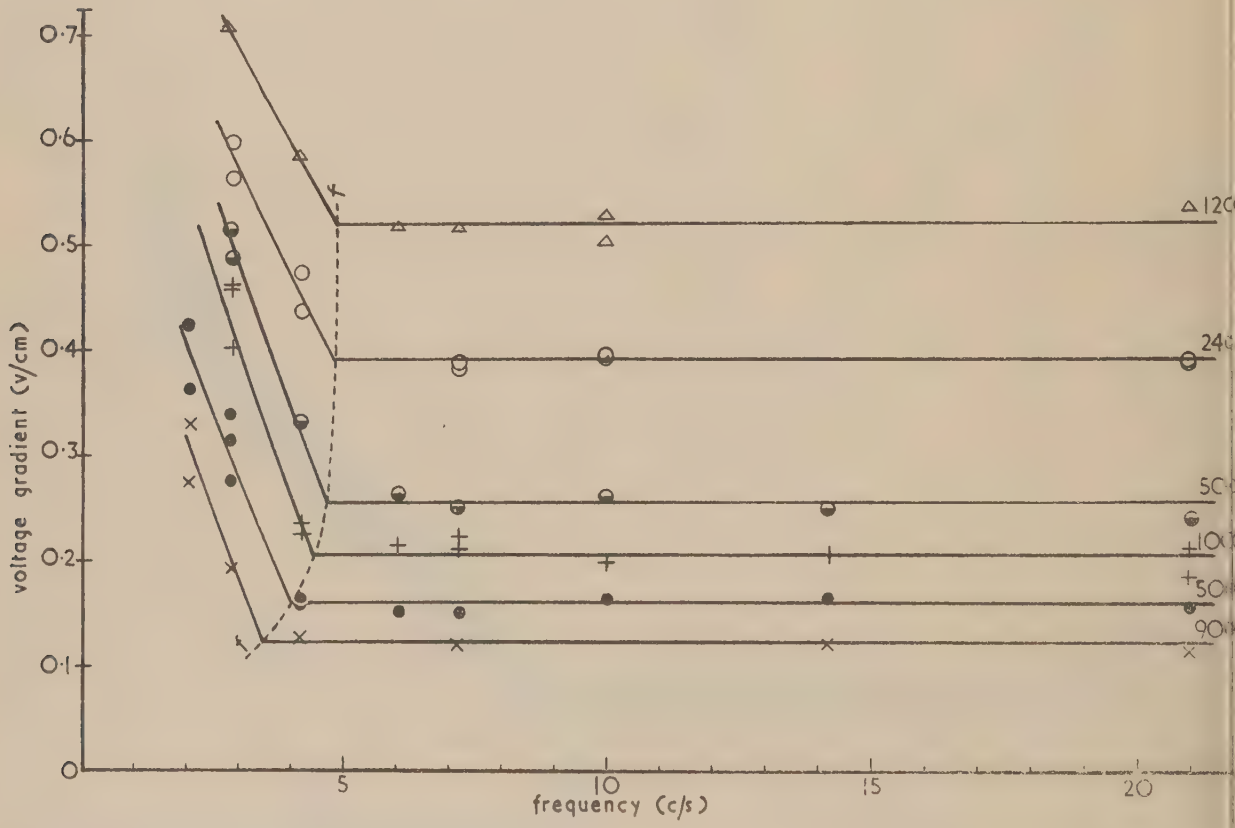
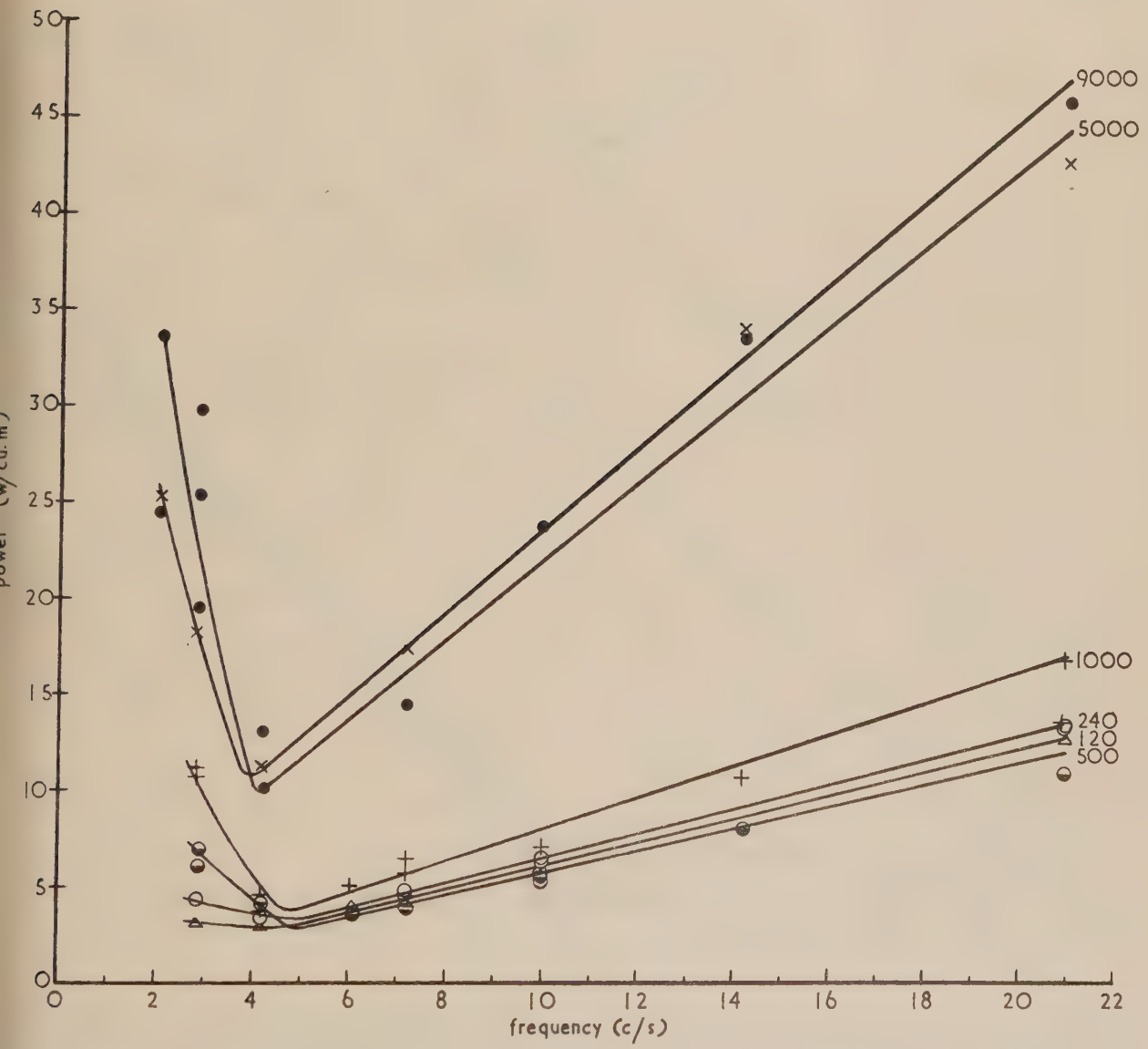


Fig. 8 The effect of frequency of pulsing on the voltage gradient for inducing electrotaxis in Standard mu with pulsed d.c.
The pulse duration used is shown on each curve.
ff: the optimum-frequency curve.

In Fig. 8, where the frequency of pulsing and voltage gradient are plotted against each other fo range of pulse durations, it is apparent that, for electrotaxis also, there is an optimum frequency bel which the voltage gradient increases suddenly and above which no detectable change is observed. A again, the optimum frequency and voltage gradient increase as pulse duration decreases; the range these frequencies lies between 3.5 and 5.0 c/s., and the voltage gradients between 0.12 and 0.52 V/c for a range of pulse durations of 120 to 9000 μs.

When watts per cubic metre are plotted against frequency (Fig. 9) the similarity to electronarcosis is again apparent but with much lower requirements consequent on the lowered frequencies and voltage gradients.

The relationships of pulse duration, frequency and voltage gradient for electrotaxis are demonstrated in a second three-dimensional representation in Fig. 10. It illustrates an interdependence of these three variables similar to that for electronarcosis.



g. 9 The effect of frequency of pulsing on the power needed to obtain electrotaxis in Standard mullet with pulsed d.c.
The pulse durations used are the same as in Fig. 8 and are shown on each curve.

The power output required for electrotaxis is represented by a curve which is almost parallel to t for electronarcosis (Fig. 11, *et*); it increases with lengthening pulse duration from 500 μs, but the fall off of the rate of increase is more strongly shown by the pronounced flattening of the curve at durati in excess of those used for causing electronarcosis.

At 500 μs there is an indication of a minimal power requirement, so that at this duration grea efficiency is obtainable.

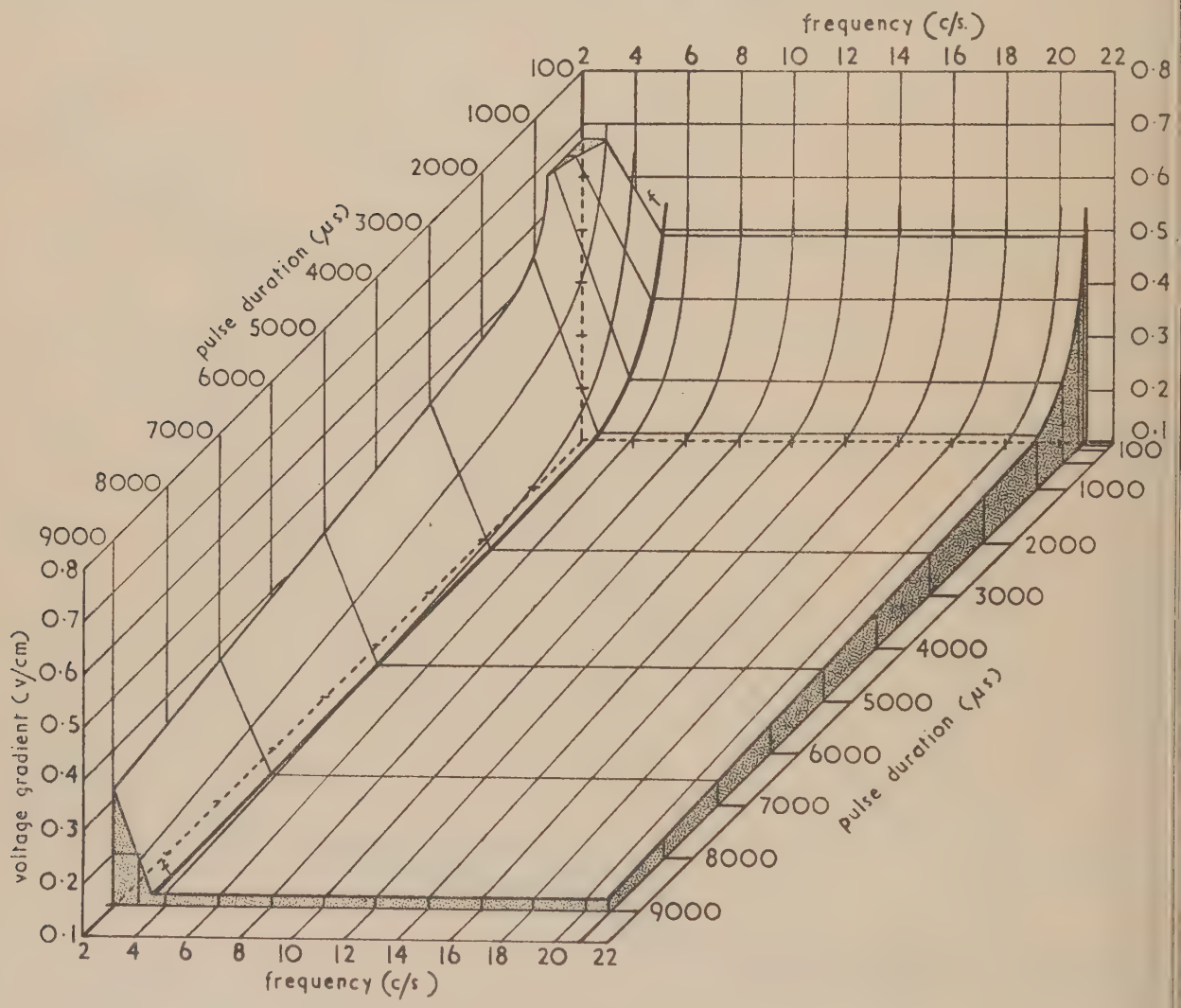
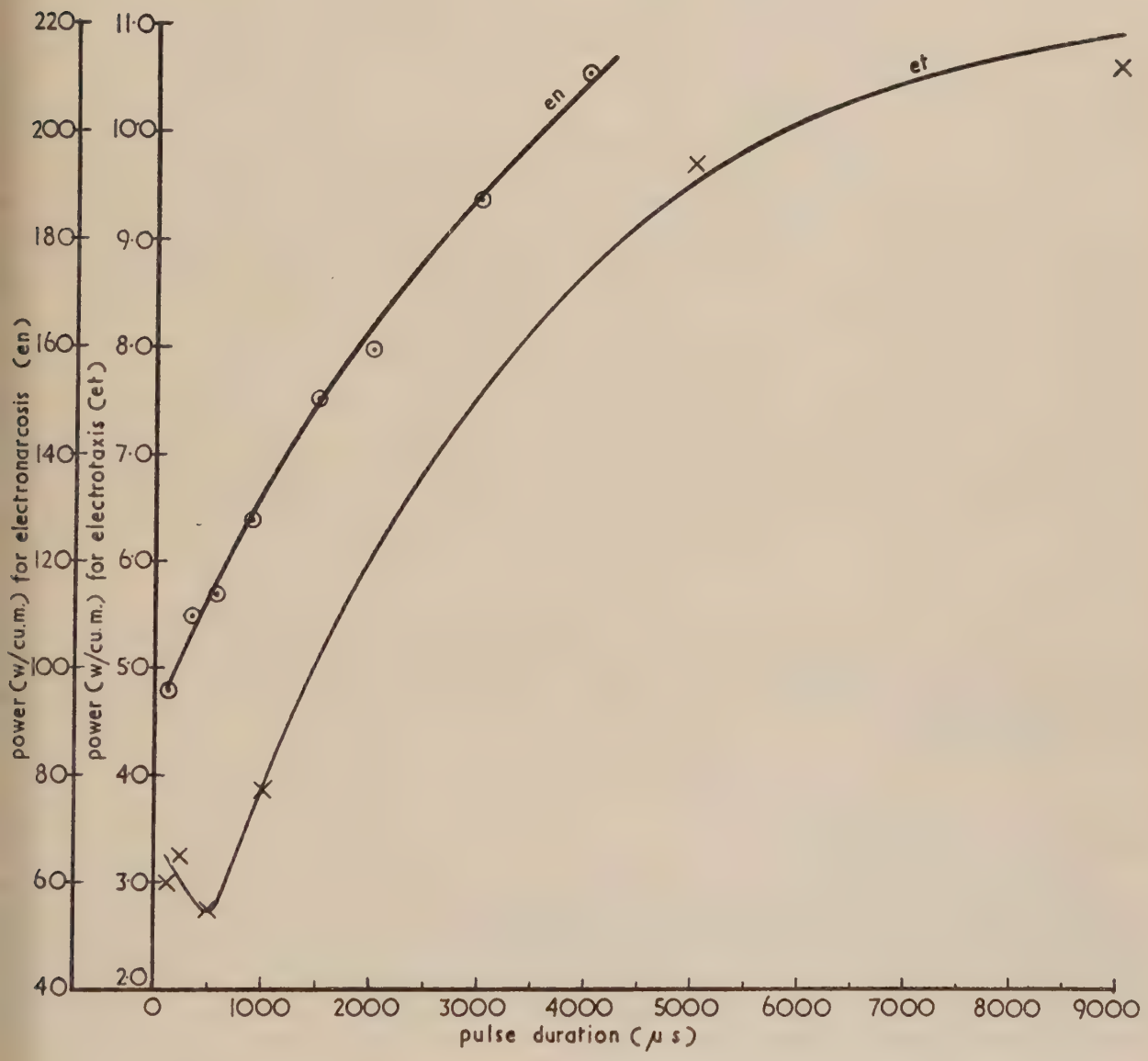


Fig. 10 A three-dimensional graph showing the inter-relationships between voltage gradient, frequency, pulsing and pulse duration when inducing electrotaxis in Standard mullet.
The figure is constructed from curve values in Fig. 8.
ff: the optimum-frequency curve.

Actual and proportionate power requirements for inducing electronarcosis with a.c., d.c. and pulsed d.c. at several pulse durations, and for electrotaxis with d.c. and pulsed d.c., in a 20 cm. fish, are presented in Table III. Values for pulsed d.c. are taken from Fig. 11.



ig. 11 The power required at the optimum frequency when inducing electrotaxis (*et*) and electronarcosis (*en*) at increasing pulse durations.

TABLE III

Comparative Power Requirements, with a 20-cm. Fish, for Electronarcosis between A.C., D.C. and Pulsed D.C. and for Electrotaxis between D.C. and Pulsed D.C.

Reaction	Pulse Duration (μs)	Power (W/cu.m.)			Ratios of Requirements		
		Pulsed d.c.	a.c.	d.c.	Pulsed d.c.	a.c.	d.c.
Electronarcosis	—	—	662	2853		1	4
	4000	210			1	3	14
	1000	134			1	5	17
	500	113			1	6	25
	250	103			1	6.5	28
	120	96			1	7	30
Electrotaxis	—	—	—	386	—	—	—
	9000	11.1			1		35
	4000	8.75			1		44
	1000	3.95			1		98
	500	2.75			1		144
	250	3.1			1		125
	120	3.4			1		114

This presentation leaves no doubt of the considerable economies obtainable by using pulsed instead of a.c. or d.c., or of the advantages which can be gained, especially in exercising electrota control, by shortening the pulse duration. The application of such pulsed d.c. to field trials wo appear to be reasonable.

Pulsed D.C. and Fish Length

The effect of fish length on the voltage gradient needed to induce electronarcosis has been determi with pulsed d.c. over a range of pulse durations (Fig. 4) for fish of Group 2, but data for Standard Fish included where applicable. The points in Fig. 4, plotted as potential difference along the fish aga fish length, may be regarded as the values at the optimum frequency; in fact, they include volt gradients found at higher frequencies, but as shown in Fig. 5 the gradients at these frequencies do change. The straight line through each set of data is the regression of y upon x.

The potential over the fish which is required for inducing electronarcosis increases with the ler of the fish; for fish of 10, 20 and 30 cm. the ratios of potential to length are approximately 1.0, 1.25 1.5 at 2000 and 1500 μs pulses, and 1.0, 1.4 and 1.8 for the short durations, but, as with a.c. and d.c., potential becomes linearly proportional if the threshold voltage is subtracted. If a number of fish various lengths are subjected to an increasing voltage gradient at a particular pulse duration and freque larger fish are controlled at a lower voltage per centimetre than smaller fish, but at a higher poten difference along their length. If the threshold voltage for the particular duration-frequency com nation is known, the voltage gradient in excess of this value will be inversely proportional to the len of the fish.

The straight line for any particular pulse duration in Fig. 4 has the formula:

$$y = bx + c \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

where y is potential over the fish, i.e., volts/cm. (V) times length (L),
x is length of fish (L) in cm.,
b and c are constants determining the position of the straight line, b being equivalent to the slope.
By substitution and rearrangement:

$$(V - b)L = c \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

When b was plotted against T (pulse duration) the result appeared to be a rectangular hyperbola to which the following applies:

$$b = f/(T - d) + a \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (3)$$

where a, d and f are constants to be found by the method of least squares,
T is pulse duration in μs, and
b is variable, depending on pulse duration, its values being weighted roughly according to the reciprocal of their variances.

The curve resulting when c was plotted against T also appeared to be hyperbolic in form, and to it the following formula applies:

$$c - k = m/\sqrt{T}$$

$$\text{or } c = m/\sqrt{T} + k \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (4)$$

where k and m are constants to be determined by least-squares method, and T is pulse duration in μs.

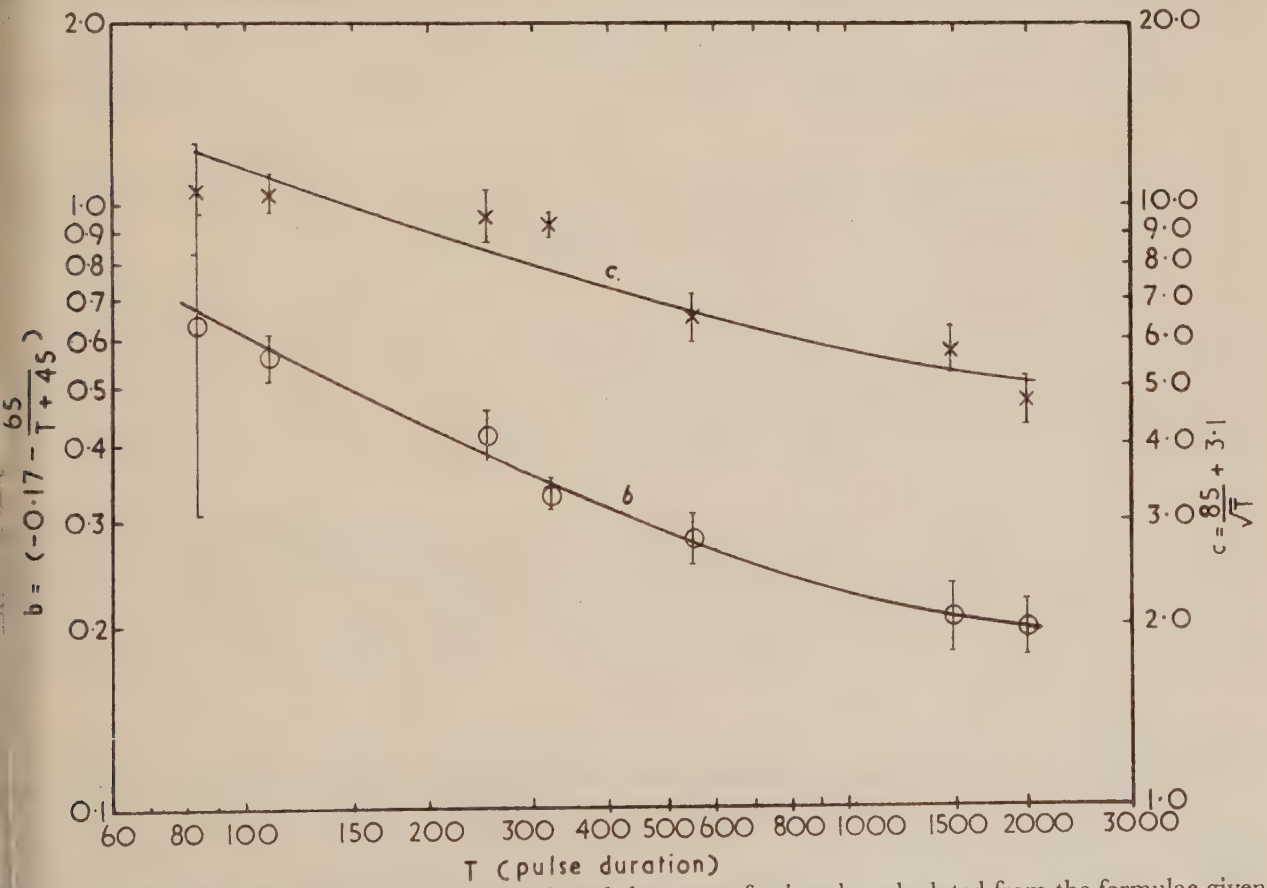


Fig. 12 The experimental values of b (o) and c (x) and the curves for b and c calculated from the formulae given in the ordinates, plotted against pulse duration (T).
The errors of b and c are shown by vertical lines.

The calculated curves for b (3) and c (4) plotted against T on a log log scale are shown in Fig. 12, a against these curves are plotted the experimental values for b (the slopes of lines in Fig. 4) and c (fr $c = (V - b)L$ [2]). The error for each point is indicated by a vertical line.

When the formulae for b and c are substituted in (2), then

$$L\{V - [a + f/(T - d)]\} = m/\sqrt{T} + k \quad .. \quad .. \quad .. \quad .. \quad .. \quad (5)$$

Substitution in (5) of the values for a, d and f (3) and k and m (4), determined for each set of da for all pulse durations (Fig. 4), gives the following:

$$L\{V - [0.17 + 65/(T + 45)]\} = 85/\sqrt{T} + 3.1 \quad .. \quad .. \quad .. \quad .. \quad (6)$$

where L is fish length in cm.,
V is volts/cm. between the electrodes, and
T is pulse duration in μs.

This equation satisfies the data from the tank experiments reasonably well and from it, given t of the unknowns, the third can be calculated, and the values so obtained are those for the optimu frequency. The behaviour of b and c at very short pulse durations is uncertain and the fitting of t formula may be satisfactory only over that range of pulse durations which this investigation shows be important and likely to be used in practice, i.e., between 400 and about 1500 μs.

The degree of fit between the calculated and the experimental results is demonstrated in Fig. (*en*), where experimental values for V are at the optimum frequency for Standard Fish (from Fig. both are plotted against T (pulse duration). The curve for experimental results (Fig. 13, *en*, solid li agrees very well with the calculated curve (dashed line) over the important range of pulse durati between 400 and 1500 μs. The calculated curve is based on pulse durations of 2000 μs and less, the experimental results above 2000 μs appear to indicate that the formula should be modified bef it is applied to longer pulse durations.

The experimental threshold voltage for d.c. is 2.4 V., whilst the formula gives 3.1 V., a value wh better satisfies the data over the critical range between 400 and 1500 μs. Further evidence is requi with very short, and also long pulses to obtain a more satisfactory final value for c.

It was possible to carry out only a brief series of experiments on the effects of fish length on gradients necessary to induce electrotaxis. Data were obtained for d.c., and for pulsed d.c. at 240 a 1000 μs, and these are plotted in Fig. 3. The voltage gradient clearly increases with length, and increase is less than directly proportional, with ratios of 1.0, 1.4 and 1.8 at 1000 μs and 1.0, 1.5 and at 240 μs for fish of 10, 20 and 30 cm. long. The variations of the ratio with pulse duration follow those electronarcosis, namely a slightly higher ratio at the short durations.

Because of the close similarity between the requirements for electronarcosis and electrotaxis it seem that the formula derived from the electronarcosis data might be modified and applied to electrota This has been done, but although there is a reasonably good fit between the experimental and calcula voltage per centimetre required to induce electrotaxis in Standard Fish (Fig. 13, *et*), the data are proba only sufficient to show that the modification is possible and would follow the lines indicated. T probable relationship is:

$$L\{V - [0.06 + 67.5/(T + 125)]\} = 31.6/\sqrt{T} + 0.75 \quad .. \quad .. \quad .. \quad (7)$$

and as with that for electronarcosis, it assumes that electrotaxis is being induced at the optimum frequen

Effects of Repeated Shocking, 'Fatigue' and Period kept in Captivity

Experiments to determine the effects of repeated shocking and 'fatigue' on values obtained for minimum response and electronarcosis were performed with a.c. and pulsed d.c. on flounder and mu

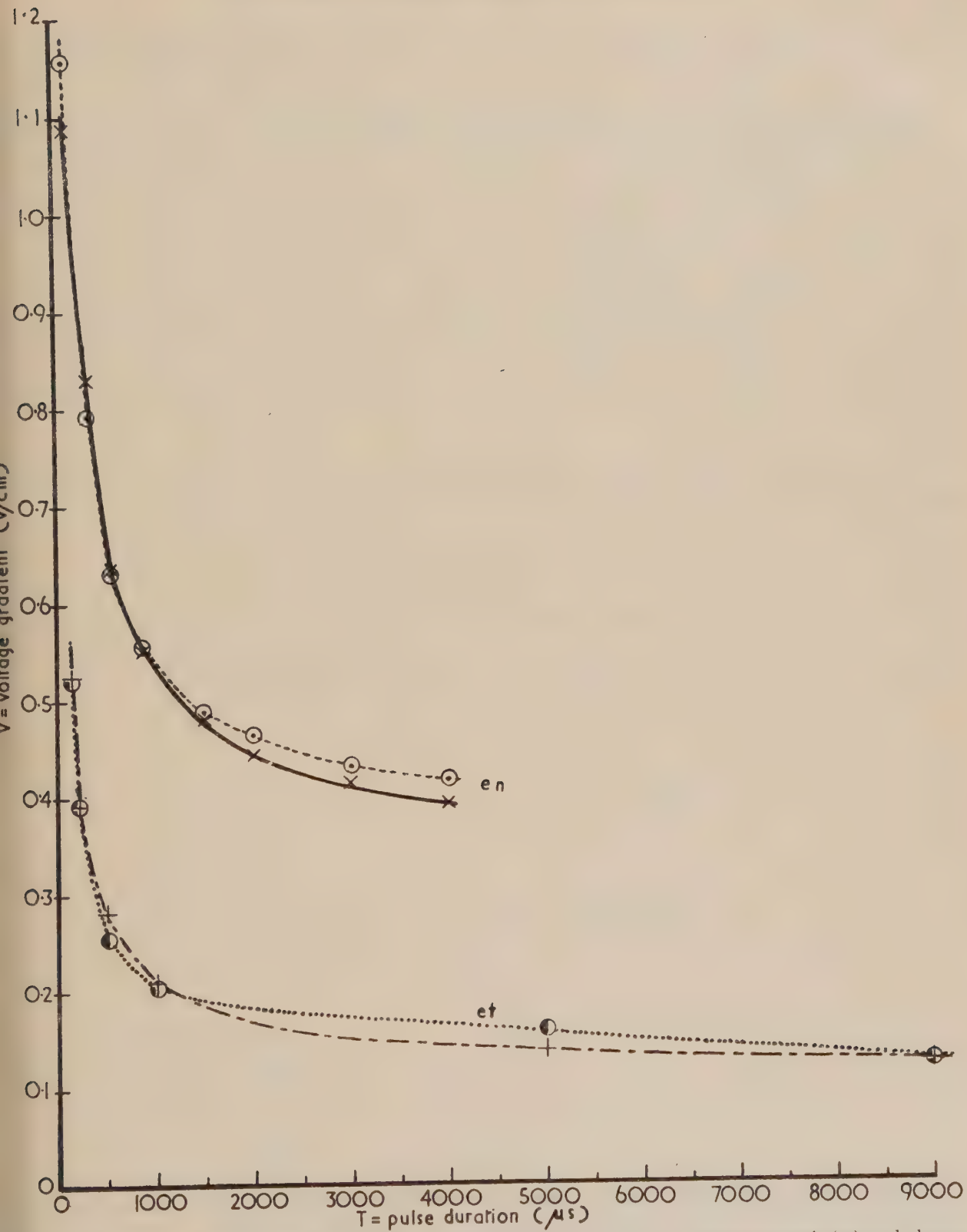


Fig. 13 The calculated voltage gradients (from equations 6 and 7) for inducing electronarcosis (*en*) and electrotaxis (*et*) at the optimum frequency in a 19-cm. mullet, compared for fit with the experimental results from Standard Fish.

⊙ calculated point for electronarcosis
× experimental point for electronarcosis
◐ calculated point for electrotaxis
+ experimental point for electrotaxis

respectively. The effects of captivity have been determined from results of experiments carried out o several months on a number of fish.

(*a*) *Repeated Shocking.* Flounder were stimulated to the minimum response and then, under const experimental conditions, were given a series of shocks separated by fixed time intervals. The inte between shocks in the first series was 60 sec. and between shocks of each of the several subsequent se was 30, 15, 10, 5 and 2 sec. respectively. Results from five fish of various lengths, tested several tin showed that when the fish was repeatedly stimulated at 60, 30 or 15 sec. intervals no change occur in its reactions over a series consisting of up to 30 shocks. Occasionally with shocks spaced at 10 intervals, and generally when the interval was reduced to 5 sec., there was moderate diminution intensity of reaction after the third to fifth shock, but thereafter the decrease, if any, was small; at 2 intervals, intensity of reaction rapidly diminished during the first four to five shocks and thereafter very weak or could not be elicited. An increase in field strength during or immediately following s a series called forth a similar diminishing pattern of reactions, and this might be repeated several ti until stimulation resulted in a higher level of reaction. As a result of these experiments, an interva 30 sec. was allowed between shocks.

To test effects of repeated shocking with pulsed d.c. four selected mullet were electronarcotised a pulse duration of 260 μs and frequency of 41 c/s. The results are summarised in Table IV.

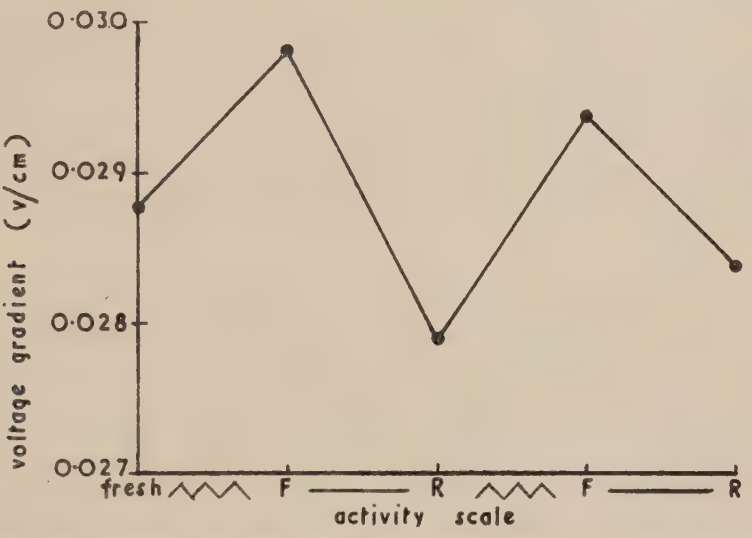
TABLE IV

The Effects of Repeated Shocking with Pulsed D.C.

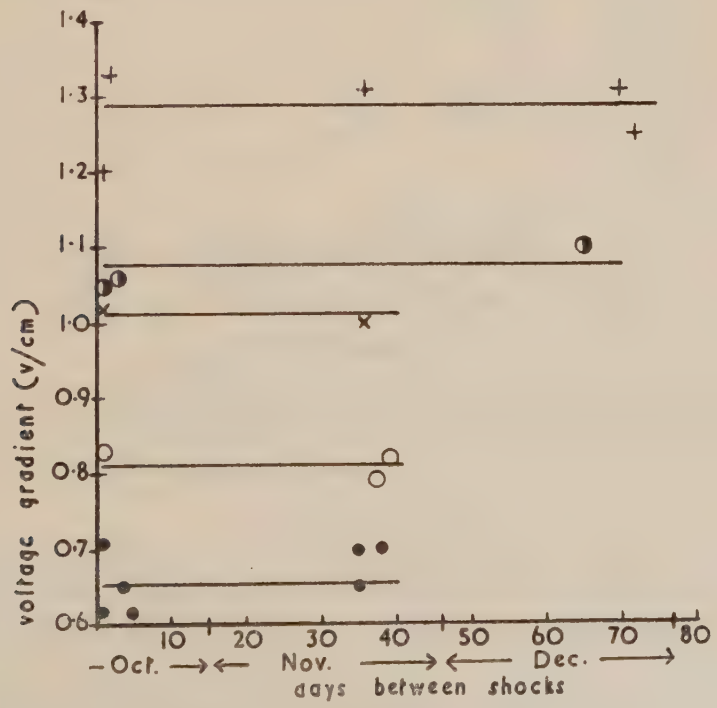
Day	Fish No.	V/cm. for Successive Tests	Interval Between Tests
1	30	1.18 1.18 1.17 1.23 1.23	5 minutes
3	,,	1.33 1.30 1.33 1.35 1.38 1.38	
1	25	1.10 1.15	
2	,,	1.26 1.20	1 hour
3	,,	1.33	
1	31	1.13	
2	,,	1.20	1 day
3	,,	1.30	
1	24	1.23	
2	,,	1.15	1 day
3	,,	1.30	

The test results obtained on the third day are rather high owing to a fault which developed in oscilliscope, but as they are consistent within themselves they have been included. The tests at 5 m intervals showed that the voltage gradient necessary to induce electronarcosis increased toward the of each series. Those at hourly, and daily, intervals showed no consistent variations. As a result of th tests, the practice was to shock an individual fish not more than once per day but, if this was unavoida intervals between shocks were of at least 2 to 3 hours.

Experience gained during electrotaxis experiments indicates, however, that change in response to ne electric field may, in fact, occur. Fish which respond firmly over a short period will not necessarily espond over a longer period. A moderate increase in field strength may then restore control, but ulti- nately the condition of the fish approaches paralysis and its movements may become uncontrollable. This behaviour appears to parallel that which occurs when flounder are shocked at short intervals with .c. in the minimum response tests.



ig. 14 The effect of rest and 'fatigue' in an initially fresh mullet on the a.c. voltage gradient required for the minimum response.
Period between shocks 15 min.
———— rest period, followed by tests on rested fish at R.
ΛΛΛΛΛΛ period of enforced swimming, followed by tests on 'fatigued' fish at F.



g. 15 The effect of length of time in captivity on the voltage gradient required for inducing electronarcosis in five mullet of different sizes with pulsed d.c.
The pulse duration is 360 μs, and the frequency of pulsing is above the optimum frequency.

(*b*) '*Fatigue*' *Tests.* One mullet was subjected to a series of tests with a.c. to determine the vol gradient required for the minimum response as the fish became exhausted. As a fresh fish, it was shoc ten times at 30 sec. intervals and then given a 15 min. rest. It was then made to swim vigorously being chased about until showing signs of exhaustion and was then subjected to a further series, e few shocks being interrupted by further enforced vigorous swimming. After a second 15 min. rest per it was shocked ten times without being chased; the whole procedure was repeated a third time.

The effect on the voltage gradient is apparent in Fig. 14. There is an increase following e period of enforced vigorous swimming and a possible tendency for 'rest' and 'fatigue' points to c closer together during the successive tests. In repeated shocking with pulsed d.c. at 5 min. inter (Table IV), there is also an increase in gradient as the series progresses. At sub-narcotic levels of shoc swimming is often extremely vigorous and, while this may not have a significant effect on the va obtained in one series of shocks, it appears to cause an increase of gradient in a number of series repea at short intervals.

(*c*) *Period in Captivity.* No special experiments have been conducted to test the effect of prolon captivity on the voltage gradient required for a given response, and data that are available are not haustive. Some experiments, however, were conducted at the pulse duration of 320 μs over a perio several months and data for fish of five different lengths have been plotted in Fig. 15 as voltage grad required for narcosis against the period in days between successive experiments. The indications that reactions are reasonably constant over the periods considered. The experience gained during experiments suggests that healthy fish kept in large tanks do not change in their reactions to ele fields over these, and possibly longer, periods. This view agrees with that expressed by Groody (1952) for *Sardinops caerulea.*

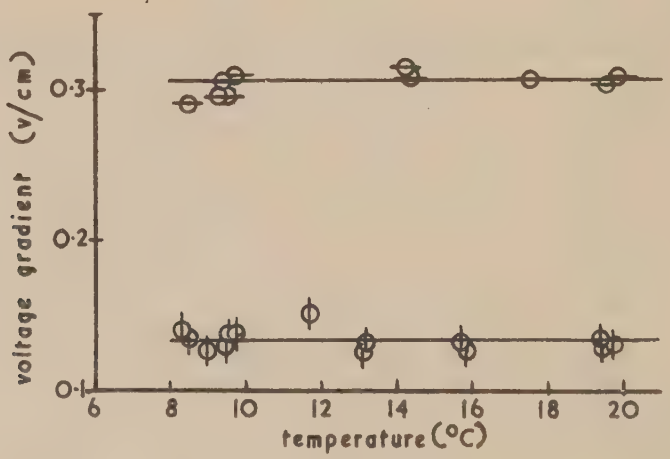


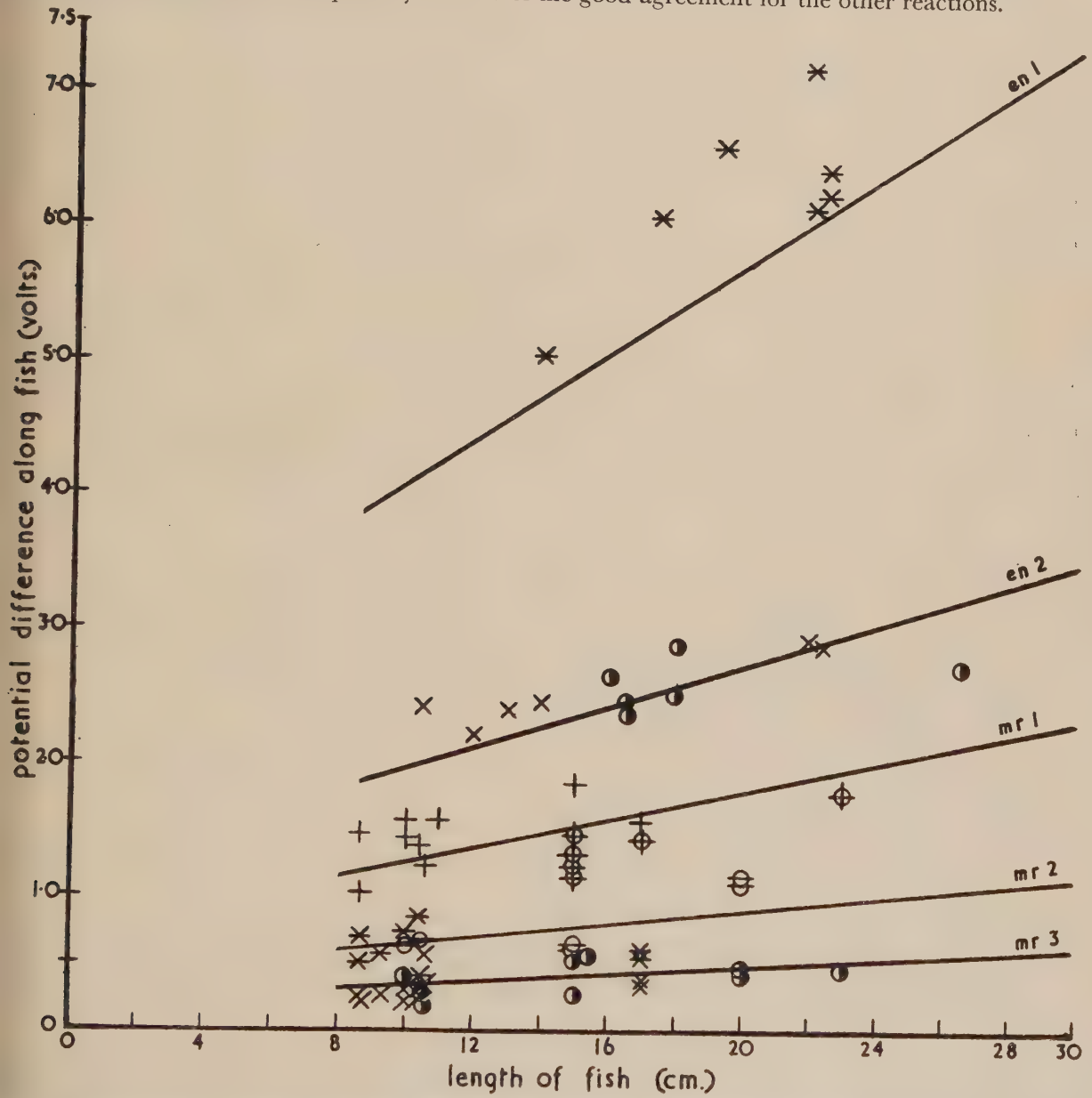
Fig. 16 The effect of temperature changes between 8° and 20° on the voltage gradients of a.c. (ϕ) and (⊖) required for inducing electronarcosis in Standard mullet.

Effects of Temperature Changes

A number of Standard Fish (19 to 20 cm. long) were electronarcotised with a.c. and d.c. over range of temperatures 8° to 20°C. Results are plotted as voltage gradient against temperature in 16. It is evident that rising temperature has not affected the gradient necessary for electronarcosis either current. Kreutzer (1950) deduced that such would be the case. It is probably safe to assume that such a range of temperature has little effect on the pulse duration, frequency or voltage grad required when using pulsed d.c. To obviate the possibility that relationships of these factors m be changed by temperature variation, experiments on Standard Fish were carried out at betwee and 10°C, which was as limited a range as was practicable.

Differences between Species

In Fig. 17 values for the minimum response and electronarcosis of bass and flounder with a.c. and d.c. are noted on the straight lines already drawn for mullet in Fig. 3. The small amount of evidence is inconclusive, but it suggests that there are no differences in the voltages needed to produce the same response in the three species. Although the diagram indicates that bass, electronarcotised with d.c., required somewhat higher potentials over their length than mullet, the evidence is probably not conclusive of specific difference, especially in view of the good agreement for the other reactions.



g. 17 The potential difference between nose and tail necessary to induce electronarcosis (*en*) and minimum response (*mr*) in bass and flounder of various lengths compared with the straight lines derived from tests on mullet (from Figs. 3 and 4).

mr1: minimum response with d.c.+ en1: electronarcosis with d.c.
mr2: „ „ „ d.c. en2: „ „ a.c.
mr3: „ „ „ a.c.

Bass: × a.c.; ✱ d.c.−, and d.c. en; + d.c.+
Flounder: ◑ a.c.; ⊖ d.c.−; ⊕ d.c.+

It would seem from the above that further experiments are necessary before attempts are made to velop apparatus for the specific selection of fish (as has been claimed possible).

DISCUSSION

Data from McMillan (1928) and Holzer (1931) for electronarcosis (paralysis) induced by a.c. freshwater and the 'equivalent solution' respectively have been converted and plotted in Fig. 18 potential over the fish against length.

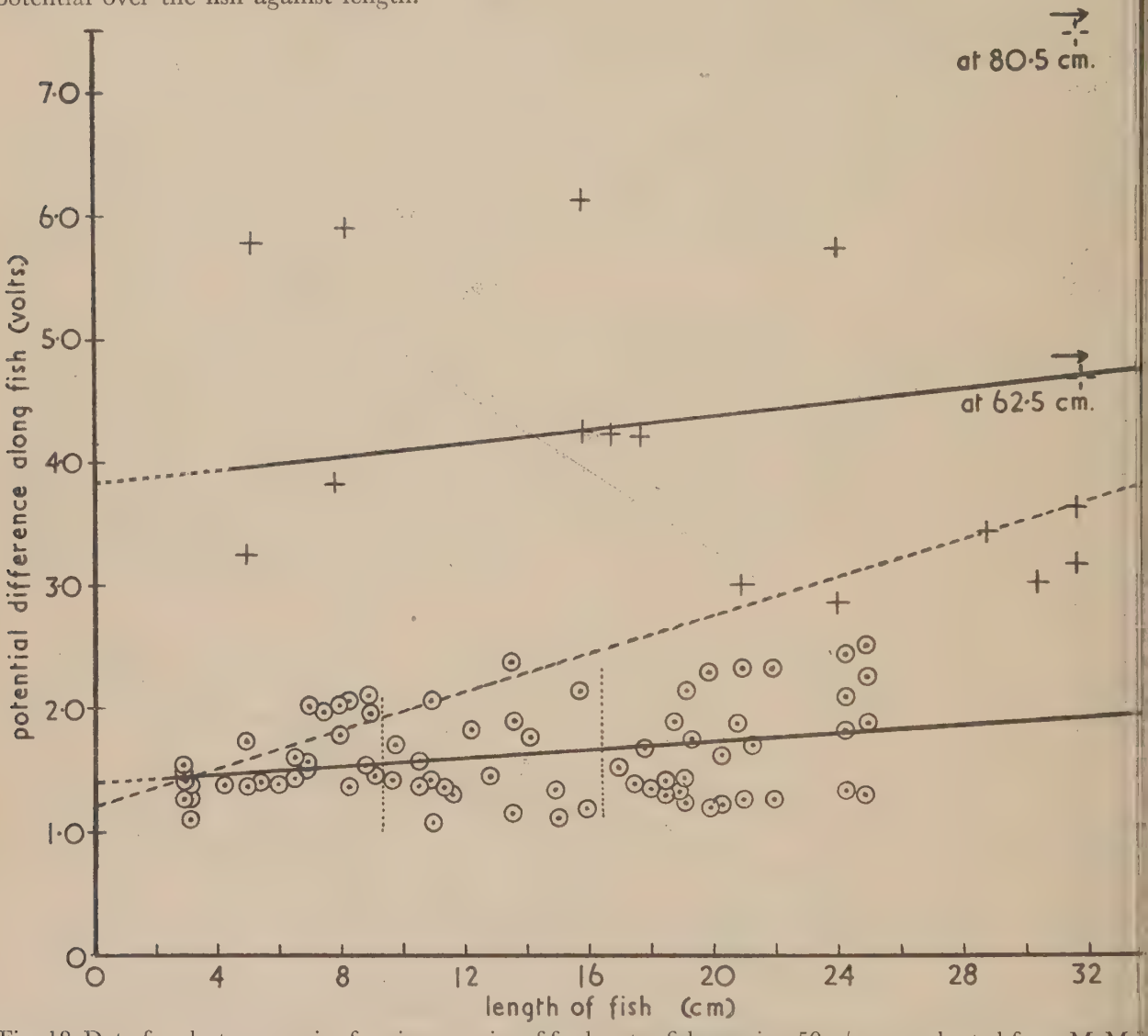


Fig. 18 Data for electronarcosis of various species of freshwater fishes, using 50 c/s a.c., adapted from McM (+) and Holzer (⊙); the dashed line is that for a.c. electronarcosis of mullet in sea-water. Ver dotted lines dividing Holzer's data indicate the possible limits of the lengths of each of the three sp he used. For discussion see text.

Both authors' investigations were carried out on a variety of species, McMillan's on Rainbow t (*Salmo irideus*), Loch Leven trout (*Salmo levensis*) and Chinook salmon (*Oncorhynchus tschawytscha*), Holz on roach (*Rutilus* sp.), carp (*Cyprinus carpio?*) and bleak (*Alburnus lucidus?*); in both cases the data w combined. The solid lines are the regression of y upon x, and the dashed line is that for electronarc of mullet with a.c. in sea-water. The lines through the two sets of points have scarcely signific slopes which contrast with the slope of the line for mullet. This indicates either a fundamental differe between sea and freshwater in the effects of size on the gradient needed for electronarcosis or a possibi that the effect of length has been masked by the use of several species. There is some indication of th groups in Holzer's data (separated by vertical dotted lines), each of which, if treated separately, mi produce a straight line of increased slope; this explanation, however, infers species differences for wh

o far, there is no real evidence. McMillan has presented only the maximum and minimum gradients t which electronarcosis occurs and the scatter makes it difficult to draw satisfactory conclusions.

Both McMillan and Holzer, and subsequently Kreutzer (1951), have produced formulae for calcuating the various quantities required in the electric controlling of fish. McMillan's formula, $g = 3.70/L$ where g is voltage gradient per inch, and L is fish length, fits his data for a.c. electronarcosis in freshvater. He calculated factors to be applied to waters of different resistivities, that for a resistivity equivalent o sea-water (10 ohms/cu. in.) being 0.219; this formula then reads $g = (3.70 \times 0.219)/L$. For a 10 in. ish, this gives a gradient of 0.081 V/in. (0.032 V/cm.); the equivalent gradient, from the present study, s 0.123 V/cm. (0.312 V/in.). Holzer has developed a much more complex mathematical treatment rom measurements of the effects of a prolate spheroid on an a.c. field in solutions with conductivities quivalent to and differing from the spheroid. The resulting formulae have been applied to fish, and, or a.c. electronarcosis in sea-water, they give a voltage gradient of 0.053 V/cm., which is of the same rder as that calculated by McMillan.

Kreutzer's formula (Kreutzer, 1951, 1954, Meyer, 1952) is:

$$R = \sqrt{\frac{I\,L\,W}{4\pi G}}$$

where:

R is distance in metres of fish from the electrodes,
I is peak current in amps entering the water,
L is length in metres of fish to be electronarcotized,
W is the specific resistance of the water in ohm-metres (0.3Ω/m.), and
G is 'body-voltage' of the species.

t is claimed that the formula is successful when used for the application of interrupted d.c. in large-scale rials. These three formulae are based on an inverse relationship between fish length and the voltage equired to induce a reaction.

The formulae for pulsed d.c., presented as an outcome of the present investigation, namely,

$L\{V - [0.17 + 65/(T + 45)]\} = 85/\sqrt{T} + 3.1$, for electronarcosis,

nd $L\{V - [0.06 + 67.5/(T + 125)]\} = 31.6/\sqrt{T} + 0.75$, for electrotaxis,

ncorporate the facts that potential over the fish needed for the reaction increases with the length of the sh and that threshold voltage decreases towards the steady d.c. value with increasing pulse duration. Therefore correspondence between these formulae and those of McMillan and Holzer cannot be exected.

A series of parallel experiments in both sea-water and freshwater would show to what degree the ifferences may be reconciled, or whether they are fundamental to the requirements of fish in the two nedia. Clarification is desirable as McMillan's and Holzer's findings have formed much of the basis of resent-day thought on the effects of electric fields on fish for both sea-water and freshwater.

All animals react to electric fields, and if these are undirectional and of certain strengths the rections include an almost consistent attraction towards the anode (Loeb, 1918; Scheminsky, Fe. and Fr., nd Bukatsch have reviewed the literature up to 1941.) In spite of their widespread occurrence few of he physiological bases of such reactions appear to be understood. The results of the present investigation, vhile not solving any problems, reveal consistent trends which are worth further examination.

Galvanotropism, or electrotaxis, has been described by Loeb (1918) as resulting from 'forced movenents'. He states that as a consequence of current flow through tissues, ionic concentrations arise at nembranes owing to their differential permeabilities and give rise to secondary chemical reactions which roduce electrotonic effects; these in turn result in "changes in the tension of associated muscles or

contractile elements, as a consequence of which motion of the organism towards one pole is facilitat toward the other is rendered difficult".

More recently attention has been focused on galvanotropism in fish, in which the response occ apparently without exception. Scheminsky (1924) claimed that it developed parallel with developm of the labyrinths and suggested that it was elicited through the effect of the current on these structur Regnard (1931), as a result of experiments in which he subjected fish to low current densities, stated t the lateral-line sensory organs function as receptors of the electrical stimulus, and further, that " canals with their mucous secretions and the organs associated with them may have considerable i portance as receptors for directional purposes . . ." Thornton (1931) also regarded the lateral-li organs as electric sense organs and suggested further that the eye may be sensitive to very low curr densities. Van Harrevald (1938) transected the lateralis, facialis and octavus nerves, which sup the lateral-line of body and head and the labyrinths, in individuals of adult *Carassius auratus* (goldfis but was still able to demonstrate the galvanotropic response. Regnard also noted that the ano response was not entirely eliminated by transecting the lateral-line nerves. Thus it would appear t other structures respond to the stimulation of the electric field.

Van Harreveld (1938) transected the spinal cord of fish and found that galvanotropism still occurr but destruction of the cord, or complete chemical narcosis of the animal, prevented it. He also claim that the reaction occurred in fish whose surface sensory receptors were removed by skinning. By plac small electrodes on the body and also dorsally and ventrally to horizontal transections through the bo wall of the visceral region, he was led to believe that the structures being stimulated were situat in the muscle of the body wall. He concluded finally that the bending of the fish's body towards anode, which is, he states, an essential part of galvanotropism, is "not caused by direct action of current on the muscles or on the motor nerves", and that "it is likely that such a reaction is a reflex . the 'galvanotropic reflex'".

The three reactions, minimum response, electrotaxis and electronarcosis, when induced by appropriate electric fields, were similar in the three different species of fish studied in the present inve gation. The relationships between the various types of electrical field used to produce a given react and between electrical requirements for inducing different reactions are, in both cases, approximat constant. These facts indicate that whatever structures are being stimulated their relationships variation of the electric field are the same; as with the information from earlier investigations vari interpretations are possible.

Burnett (1952) pointed out that 'strength-duration' curves for an entire fish (the freshwater *Galax attenuatus* and *Anguilla dieffenbachii*) conform to those for nerve-muscle preparations (Katz, 1939). Simi curves were illustrated, but not discussed, by McMillan (1928) and Holzer (1931), and van Harreve Plesset and Wiersma (1942) drew them for the electronarcotization of dogs. Typical 'strength-durati curves obtained from the present study are given in Fig. 13. Van Harreveld *et al.* from a chronaxie 150μs concluded only that "highly excitable structures, nerve fibres or cells are stimulated" and s gested that stimulation is of peripheral nerves. The chronaxie for *Galaxias* (converted from that fo triangular pulse to the equivalent of a square-shaped pulse—see Katz, 1939, p. 27) is between 500 a 600 μs, and that from Fig. 13, using the d.c. rheobase gradient of 0.29 V/cm. calculated for a 19 c fish from Fig. 4, is approximately 260μs. The latter figure, and to a lesser degree Burnett's, also indica the probability that highly excitable structures are being stimulated.

The decreasing intensity of the jerk, or minimum response, with stimuli repeated at intervals of sec. or less, and possibly the decrease in electrotaxis over an extended period, closely resemble t phenomenon of habituation (Thorpe, 1950). On the other hand, if van Harreveld's interpretation th activity results from electrical stimulation of reflex arcs is correct, such fading in intensity of reacti may well be the result of too close repetition or prolongation of the stimulus. This may be true since slight increase in field strength will induce a further series of diminishing responses; moreover, t

equency of stimulation may be regulated to produce responses which, though weak, continue to be cited with little or no change over a long series. Thorpe mentions a possible distinction between the elatively transient effects of sensory fatigue and the persistent effects of central (nervous system) abituation", but points out that it is not known whether "sensory 'accommodation' or 'fatigue' on the he hand and central nervous system habituation on the other are ultimately expressions of the same ndamental property . . ." Thus, it does not appear possible to distinguish between what may be the sult of habituation to stimuli and what may be due to 'accommodation' or 'fatigue' of nervous elements; e reactions of the fish to repetitive stimuli are explainable by either.

There remains a possibility that muscle is being directly stimulated. In a fish which has been made swim vigorously, a higher voltage gradient is required to elicit the minimum response than is required r the same fish in a fresh condition or following a period of rest. There is also a tendency for the re- uired gradients of successive 'rest' and 'fatigue' tests to approach one another (Fig. 14). These effects ay be due, either singly or in combination, to muscle fatigue or to the production and accumulation metabolic substances, e.g., lactic acid (Hoar, Black and Black, 1951, p. 104), causing a complexity of nditions requiring higher gradients. The evidence is more convincing if the optimum frequency at hich electronarcosis is induced with pulsed d.c. is regarded as the fusion frequency of muscle con- action. At 110 μs pulse duration this frequency is 35 c/s. combined with the high voltage gradient of 09 V/cm., and at 4000 μs is 17.5 c/s. and 0.4 V/cm. The lowered frequency and voltage gradient at e longer duration is consistent with effects of muscle stimulation. The upward trend of the required adient at frequencies less than the optimum frequency is also consistent: under these conditions con- actions fuse when the increased voltage is sufficient to overcome the relatively decreased effect of petitive stimuli spaced at too great intervals. The similarity between the electrical requirements eeded to induce electrotaxis and electronarcosis is possibly due to similar structures being stimulated. lectrotaxis is obtained when repetitive stimuli, of a strength and frequency sufficient to produce a series individual responses, are combined with a mechanism like van Harreveld's 'galvanotropic reflex' to nsure that the fish is heading towards the anode.

When flounder are stimulated to the minimum response with the longtitudinal axis of the body at ght angles to the field the response is as strong as when the head is towards the cathode; mullet, on e other hand, require a much higher field strength when broadside on. Since the body in this osition is at right angles to field direction, it can be assumed that the stimulation is through segmental erves rather than the central nervous system. If the sensory nerves are being stimulated, then the sponse is possibly of a reflex nature; but in the case of the motor nerves the response is probably due their stimulation being transmitted directly to the muscles. In flounder the segmental nerves are nger than in the mullet and would be stimulated at a comparatively lower gradient than is needed the round fish. Thus, there is an indication that direct stimulation of the segmental nerves may itiate at least the minimum response.

More data from experiments with more precise control of the electric fields and the movements the fish are needed in order to clarify the physiological reasons for the responses of fish to electric fields. seems possible that the present techniques could be further developed to produce much useful formation.

SUMMARY

Marine fish have been subjected to uniform electric fields of 50 c/s. a.c., d.c. and pulsed d.c. in perimental conditions and comparisons of the effectiveness of these currents in producing three reactions, e minimum response (a jerk at make of current), electrotaxis and electronarcosis, have been made. ost of the experiments have been made with two groups of mullet (*Mugil auratus* Risso): one, the Stan-. rd Fish, 18.5 to 20.6 cm. long, was used to determine the relationships between pulse duration, quency of pulsing, voltage gradient and power required to induce electrotaxis and electronarcosis, d the effect of temperature on the requirements for narcosis with a.c. and d.c.; the second, or Group

2 Fish, 8.6 to 30.2 cm. long, was used to find how the voltage required to produce the several reacti depended on the length of the fish and how it varied with fatigue and duration of time in captivity.

2. Experiments were carried out to find whether the voltage gradient of a.c. and d.c. required to indu the minimum response and electronarcosis varied between species. The evidence suggests that there little if any difference between bass (*Morone labrax* (L.)), flounder (*Platichthys flesus* (L.)) and mullet (*M aurutus* Risso).

3. In a d.c. field, the voltage required to elicit the minimum response when the head is pointing wards the anode (d.c.+) is double the voltage required when the head points towards the cath (d.c.—); the gradient required to produce electronarcosis in free-swimming fish is nearer what wo be needed with d.c.— than with d.c.+. A.c. (r.m.s. values) induces the minimum response at appro mately one-half the voltage gradient needed for d.c.— and one-quarter of that for d.c.+; for elect narcosis rather less than half the d.c. gradient is required. The ratios of the voltage gradients (and powe necessary for inducing the minimum response and electronarcosis are approximately the same w either a.c. or d.c. Electrotaxis values with d.c. are intermediate between those for the minimum respo and electonarcosis.

4. The voltage gradients of a.c. or d.c. needed to induce electronarcosis appear not to depend on temperature, but higher gradients are needed to elicit the minimum response in a fatigued fish than a rested or fresh fish.

5. Requirements for electrotaxis and electronarcosis induced with pulsed d.c. conform to a sim pattern. For a given pulse duration, there is an optimum frequency of pulsing. At higher frequenc the voltage gradient required does not increase, but the power increases proportionally with the frequen at frequencies less than the optimum, both gradient and power must be increased to obtain the des effect. As the pulse duration is lengthened, lower voltage gradients and frequencies are required elicit a given response. The power needed varies with these factors, and in general it increases w pulse duration, although there is an indication that the power requirement for inducing electrotax least at the pulse duration of 500 μs.

6. An increase in the length of fish demands an increase in the potential difference between nose tail to induce any of the three reactions with the three types of electric field used; the increase of poten required is less than directly proportional to the increase in length (but becomes so if the thresh voltage is subtracted); hence long fish require a higher potential over their length, but a lower volt gradient, than short fish. Empirical formulae have been evolved relating the voltage gradient volts/cm.) and pulse duration (T, microsecs.) required to electronarcotize or induce electrotaxis in of given length (L, cm.) at the optimum frequency; these formulae are, for electronarcosis,

$$L\{V - [0.17 + 65/(T + 45)]\} = 85/\sqrt{T} + 3.1$$

and for electrotaxis,

$$L\{V - [0.06 + 67.5/(T + 125)]\} = 31.6/\sqrt{T} + 0.75$$

so that, at an optimum pulse duration of $T = 500$ μs, these formulae reduce to

$$\text{Electronarcosis,} \quad V = \frac{6.9}{L} + 0.29 \text{ and}$$

$$\text{Electrotaxis,} \quad V = \frac{2.2}{L} + 0.17$$

The requirements for inducing electronarcosis with pulsed d.c. appear not to be affected by the time fish is held in captivity, provided that it is healthy. The possible physiological reasons for the respo to electric fields are discussed.

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